A STUDY OF FERTILITY

and

RELATED CONDITIONS IN THE GUINEA PIG

by

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1929.

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Part II

A STUDY OF FERTILITY AND RELATED CONDITIONS IN THE GUINEA PIG

INTRODUCTION

Fertility in animals is a very complicated characteristic. It has been differently defined by various authors; for instance, Pearl and Surface (1909) refer to fertility as the total reproductive capacity of pairs of organisms in terms of offspring born. On the other hand Crew (1925) considers fecundity as the term to express the potential reproductive capacity of an individual which is measured by its ability to elaborate functional gametes, and "fertility as the term used to define the ability of a pair (male and female) to produce living offspring and is measured by the rate at which these are produced...,". Fertility is thus used as a term to designate net fecundity. In the present paper it is used in a still more exacting sense to designate the number of living offspring raised to weaning per pair of individuals mated. It is obvious that fertility in this sense is influenced by (1) the frequency of litters, (2) size of litters in sense of ova produced, (3) intrauterine mortality, (4) mortality at birth, and (5) mortality between birth and weaning.

By making reciprocal matings between crossbred and inbred males and females in suitable comparisons with inbred and crossbred lines of guinea pigs, Wright (1922) has been able to estimate the relative importance of the kind of breeding (i. e. inbreeding or crossbreeding)

of the dam or the sire or the young on certain of these characteristics. The frequency of litters was found to depend primarily on the breeding of the sire and secondarily on that of the dam, while the breeding of the young appeared to be of no importance. The size of litter was affected wholly by the breeding of the dam and not at all by the way the sire or young were bred. There appear to be no published records from which estimates of the importance of breeding in relation to intrauterine mortality can be determined but the mortality at birth, which partly includes intrauterine mortality, especially during the later periods of gestation, was found by Wright to be almost entirely a maternal affair, at least as far as it is hereditary at all. The mortality between birth and weaning was found to depend largely on the breeding of the young but the breeding of the dam was also an important factor.

In addition to the influences mentioned as acting on the total number of young raised per mating, it is quite obvious that numerous other factors enter. For instance, the frequency of litters, which was found to be primarily dependent upon the vigor of the male, is also obviously dependent upon the presence of normal viable ova in the proper stage of development in the female tract. The size of litter is dependent upon the number of ova produced and the relative viability of the ova associated with fertilization by normal sperms. Marshall (1904) and Hammond (1914

and 1921) have shown that the limiting factor in fertility is the number of ova produced by the female, as the male parent either produces sufficient sperm to fertilize all the ova or all of his sperm are nonviable, in which case the mating is sterile. The relative frequency of breeding as well as the age or condition of the sire as influenced by environment and season may have some effect upon the viability of the spermatazoa. Lloyd-Jones and Hays (1918) and Hays (1918) found in studies at the Iowa Experiment Station that frequent matings of male rabbits reduced the size of litter only toward the end of the period. Hammond (1914), however, found no reduction in the fertility of the females after thirty-seven services by one male within eight hours (rabbits). These are exceptional cases and under ordinary conditions the dam is clearly of primary importance in regard to litter size, which is fundamentally related to the number of ova produced at the time of ovulation. This was the conclusion of Heape (1899), Marshall (1904, 1922, etc.), and Nichols (1926 etc.), and others. It is only possible to speculate as to the factors which influence ovulation.

Heredity no doubt bears an important part as Wright (1922) in the guinea pig, Feldman (1925) and King (1924) in the rat, Surface (1909) in swine, and others have shown that there are considerable differences in the size of litters produced within different families and strains, but the number of ova are apparently influenced by other conditions, such as the age of the dam, diseased condition, and environment and season. Nichols (1928) found the following

factors of importance as influences on the degree of fertility in sheep: (1) genetic factors (breed differences), (2) age of dam, (3) time of service, (4) nutrition, (5) environment, (6) lethals; their effect being considered primarily in connection with the number of ova produced - the limiting factor in fertility. The quantity and occurrence of ovulation seems to be a composite of numerous influences, a deficiency of any one preventing or reducing ovulation.

Several investigations on intrauterine mortality in different mammals have been somewhat variable in their conclusions. Corner (1923) working with swine came to the conclusion that the factor responsible for the cases of intrauterine mortality which he observed were not due to faulty implantation or abnormalities in the uterine mucosa, while McDowell (1924), working on intrauterine mortality in mice concluded that the factors affecting it were nongenetic. Hammond (1921) suggested adiposity, inbreeding or lethals. The opinions and conclusions of many others could be brought in but they would be of little value further than to indicate the diversity of views. There are many cases of lethals operating in mammals which have been described particularly by Mohr (1926), Wriedt (1925), and others in several publications. Probably the most familiar case of lethal factors in mammals is that of the yellow mouse. The lack of homozygous yellows was first pointed out by Cuenot (1905) and later suggested as being lethal by

Castle and Little (1910). This was confirmed by Kirkham (1919) and Ibsen & Steigleider (1917).

The mortality at birth and after birth are no doubt influenced by several conditions, including the length of the gestation period, environmental conditions, and the age and condition of the dam; the heredity of the young being of considerable importance in case of mortality after birth. These factors are probably more or less interrelated and interacting; for instance, size of litter affects both the mortality at birth and after birth.

In studies so far conducted of the behavior of genetic characters relating to fertility in farm animals little progress has been made beyond the discovery of lethals. Rommell and Phillips (1907) found productiveness a character in Poland China swine which was transmitted from mother to daughter, but Pearson (1907) failed to find a significant parental correlation in regard to size of litter. Pearl (1912) and others reported definite Mendelian factors responsible for egg production and other factors related to egg production. More progress has been made with fowls in this respect than with any of the other classes of farm animals. It is generally recognized that though an individual may genotypically be very fertile, it must have optimum environmental conditions for maximum reproduction. Marshall (1922) states that Aristotle commented on the increased fertility of sheep in a favorable environment, and Heape (1899) found that the district, type of soil, season, manage-

ment and quality and quantity of food were related to fertility. Numerous others have made similar observations. Darwin (1905) attributed the increased ferility of domestic as compared with wild animals to a long habituation to a regular and copious food supply without the labor of seeking it. The studies of Evans and associates (1922, 1923 and 1925), Sure (1924) and others have definitely shown the necessity of the presence of an essential food substance for normal reproduction, and various investigators have brought out the importance of relatively large amounts of vitamin B for successful lactation and the rearing of young, though Miller (1927) found in studies with rats that the percentage of vitamin B in a ration for successful gestation and lactation was no greater than that needed for normal growth.

In numerous studies of the factors influencing the mineral metabolism of animals, Hart (1925) at the Wisconsin station, found that minerals, especially calcium and phosphorus, were necessary for optimum reproduction. Similar conclusions were obtained by Eckles, Becker, and Palmer (1926) in experiments with cattle. As the amount of calcium assimilated is associated with the availability of the antirachitic vitamin, a definite relation between fertility and the sunlight, the natural source of this substance, seems to be indicated.

A relation between the season and the breeding of certain animals is generally known. The ewe and bitch furnish the most outstanding examples of season of breeding in the common domestic animals. The cow and sow come in heat rather regularly over the

entire year, and the mare somewhat less regularly. The exact factors associated with the occurrence of periods of heat have not yet been discovered, but such things as temperature, length of day, intensity of sunlight, feeds associated with the season, etc. have been suggested. Oestrum was definitely shown to be the result of the presence of the liquor of the Graafian follicles of the ovary by Allen et al (1924) and by others. Similar changes have been produced in spayed and immature female rats (Allen and Doisy, 1924) and in other animals by subcutaneous injections of small amounts of the liquor folliculi from the Graafian follicles of the rat, sow, ewe, cow, hen, and human ovaries. Tho this work has received confirmation in many investigations with the rat, Asdell and Marshall (1927) working with dogs and rabbits concluded that a further factor than the follicular hormone was necessary to bring about the complete production of all the changes and conditions associated with oestrum. This was confirmed by Parkes (1926-27) and Parkes, Fielding and Brambell (1927).

The definite changes in the genital tract associated with oestrum have been studied by many investigators working with most of the common mammals. The more recent have been mainly concerned with the identification of oestrum by the vaginal smear method, first described by Stockard and Papanicolaou (1917) for the guinea pig. A few of the more important contributions along this line in the guinea pig are the extensive works of Loeb (1911, 1914, 1917, etc.) and the papers of others including Courrier (1923), Sun (1923), and Guttmacher (1925). Contributors on the female sexual cycle in other animals include mare (Seaborn 1925), cow (McNutt 1924, Murphy 1926, Zupp 1926, and Hammond 1927), ewe (Marshall 1922), sow (Corner 1921 and McKenzie 1926), dog

(Evans and Cole 1927), ferret (Robinson 1918), opossum (Hartman 1923), rabbit (Wood 1925, Hammond 1925), Rat (Long and Evans 1922), and in the mouse (Allen 1922, Parkes & Bellerby 1926 and 1927).

Notwithstanding these investigations practically no light has been shed on the natural factor or factors causing the maturation of the ova or influencing the number which are produced at a time. A common practice, especially with ewes, known as flushing, which is believed by the practical sheep breeder to increase the number of lambs, has been questioned by some, while others support it. Marshall (1908) found in a study of flock records that the percentage of lambs born was as a rule highest amongst sheep which had been subjected to a process of artificial feeding, and Loeb (1921) in controlled experiments with guinea pigs prevented the maturation of ova by subjecting the animals to rigorous undernourishment, which caused the follicles to become atresic before attaining medium size. The Missouri Agricultural Experiment Station (1924) found an effect of the plane of nutrition on the fertility of swine. Two sows on a medium plane of nutrition produced 74 pigs while similar sows on high and low planes produced 54 and 29 pigs respectively.

The preceding discussion of fertility and the possible factors affecting it is given for the purpose of indicating the diversity of the factors which influence fertility, and it is not to be considered in any sense as complete. The importance of these and probably other factors must be taken into account in the planning and conduct of controlled experiments designed to study the influence of a particular factor on fertility. The uncertainty that all factors are accounted for in a controlled experiment is obvious and the difficulty

of obtaining such control would have made an experiment of that nature impossible under the conditions that the following study was conducted. Access to eighteen years records on over 30,000 guinea pigs was obtained and it was felt that such offered an unusual opportunity for a statistical study of environmental and seasonal variations in fertility.

PLAN

The present study was made to determine the relation between the various measurable components of fertility and related factors in guinea pigs and to gather some idea of the relative influence of prenatal mortality on the fertility of matings within and between inbred families. The study thus consists of two parts, Part 1 being a statistical study of the records of the guinea pigs produced in the inbreeding experiment of the Division of Animal Husbandry, U. S. Department of Agriculture at Beltsville, Md., from 1906 to 1924, inclusive. Part 2 consists of a comparison of the number of corpora lutea found in the ovaries of the females of the inbred families with the number of normal and abnormal fetuses observed in pregnant females killed before parturition. For Part 1 the records of the 30,857 guinea pigs born in 11,945 litters in the inbreeding experiment from September 1906 to December 1924 were tabulated for each of the 220 months according to the family, generation, mating and litter number, date of birth, birth and weaning weights, mortality, etc. After making necessary corrections to eliminate nonseasonal factors as far as possible, eight indices were calculated for each month and correlations determined between the different indices within each month and between

each of the four preceding and succeeding months. In addition the data were also tabulated according to birth rank to obtain an estimate of the relative comparison of young born in first, second, third, etc. litters. For Part 2 there were selected 351 females from four inbred families, and from crossbred and control stocks. These were mated with males from each of the five inbred families and killed just before parturition in order to make the corpora lutea counts and determine the amount of prenatal mortality in females from each of the inbred families and the other stocks when mated with males from each of the five inbred lines which were being carried in the inbreeding experiment. In connection with this work the uteri and ovaries of pregnant females dying from all experiments were preserved in formalin and examined as time permitted.

PART I.

STATISTICAL STUDY OF THE RELATION BETWEEN VARIOUS EXPRESSIONS OF FERTILITY AND VIGOR.

The records on which this portion of the study is based were obtained in the inbreeding experiment which was planned and begun in 1906 by George M. Rommel. The work was started at the experiment station at Bethesda, Md., but in 1911 was moved to Beltsville, Md. Due to the change in the location and the necessity of making some modifications in the equipment from time to time, conditions were not as uniform as might be desired, but from the standpoint of the study of the reaction to variations in the environment it may be of some advantage. Moving the stocks, together with necessary changes in the super-

vision of the colony and unusual seasonal conditions which made alterations in the food supply necessary, may account for some of the irregular relations between different monthly indices observed in Chart XII, p. 51. The fact that the entire stock was showing a slow but gradual decrease in vigor throughout the entire period over which these records were taken as a result of inbreeding should not be overlooked. The linear equations for the decline in most of the factors studied have been calculated by Wright (1922) in connection with his analysis of the effects of inbreeding in the stock. The history, method of mating, feeding, care, and data recorded are briefly discussed in that publication. It will be sufficient to state that all matings were between brothers and sisters selected from the same litters and were usually made at 33 days of age, the time of weaning. The basic ration used throughout has consisted mainly of oats supplemented with hay and green feeds. Litters were recorded on the date of birth and descriptions made of the number, weights, sex, and color markings of each individual. Weights were again taken at weaning (33 days). Those born dead or dying between birth and weaning are so recorded. Records of the date on which each pair were mated are also available.

Method of Determining the Monthly Indices.

In order to determine the relations between the different characters eight indices were calculated for each month from August 1906 to December 1924. The monthly indices included litters per 100 matings, average size of litter, sex ratio, average birth weight, average gain between birth and weaning, per cent born alive, per cent raised of those born alive, and number raised per 100 matings. The basic data for the

calculation of all the indices except litters per 100 matings was transferred from the original records to Hollerith cards. A card was punched for each individual, giving the family, generation, mating, and litter number, the month and year of birth, size of litter in which born, and for the individual its number, sex, birth weight, 33-day weight and whether born dead, died between birth and weaning, or raised to 33 days of age. The cards bearing the data were then sorted and tabulated with the usual tabulating machinery in desired groups.

The necessary steps and means of calculating each index which also served as definitions, were as follows:

Litters per 100 matings.- This was the index indicating the frequency at which litters occurred and was calculated as 100 times the number of litters born in a particular month divided by the number of pairs mated in that month. It was, however, necessary to correct for certain irregularities to make the indices comparable from month to month. As nearly all matings were made between brothers and sisters at 33 days of age when the males at least and usually both males and females were sexually immature, a new mating was not counted until two months after it started. The basis for the correction was Wright's (1922) findings that the minimum age at which males may sire litters is about 60 days, and the average age at which first litters were born was 5.9 months. Mature animals also required some time to get acquainted in new matings. Matings were stopped in the month after that in which the female died or was removed and two months after the male died or was removed. After dividing 100 times the number of litters born in each month, as determined from the Hollerith card count, by the number of matings in that month, the quotient was corrected to a 30

day month by multiplying by 30 and by dividing by the number of days within the particular month. The reason for this is quite obvious as in a 31-day month there are 31 chances for litters to be born as compared with 28 in February of a nonleap year.

Size of litter.- The average size of litter was readily calculated from the total number of litters of all sizes and the number of individuals born in a particular month.

Sex ratio.- In this study the sex ratio was expressed as per cent males rather than by the more customary means - the number of males per 100 females. The merits of this method are being recognized by others as the more acceptable. It gives a better and more direct indication of the makeup of the population, and the probable error may be easily and accurately calculated.

Birth weights and gains.- In deciding upon a proper means of determining the average weight for each month a number of complications enter. Weights show a great deal of variation which is in part related to the size of litter, fate, and sex. The birth weights were calculated separately for each litter size, sex, and for those born dead, dying between birth and weaning, and for those raised to weaning, but since gains up to weaning were likewise to be obtained, it was decided to use the average birth weights of those which were raised to weaning, corrected to eliminate the effect of size of litter and sex, as the monthly index. This entirely eliminated any complications from abortions and premature births and makes the weights applicable to the individuals which survived to weaning, and further, it gave the birth weights of the same individuals that the gains applied to. In cal-

culating the gains, the average 33-day weight for each month, corrected for size of litter and sex, was first determined and the difference between the corrected birth weight and the corrected 33-day weight gave the gain for the month. The gains for a particular month referred to the calendar month in which the animal was born rather than during the month in which the gain was made; thus, the relation between birth weights and gains is not lost. Both the birth weights and the 33-day weights were corrected by an artificial means for the purpose of eliminating the effect of size of litter and sex. The indexes must therefore be recognized as modified to this extent. The basis for the corrections is described later.

Per cent born alive and raised.- The percentage born alive and the percentage raised of those born alive are also affected by the size of litter, and a comparable method for the elimination of such effect was devised as described below. The months apply to the month of birth for the percentage raised as in the case of gains.

Young raised per 100 matings.- The young raised per 100 matings may be termed "net fertility". It is simply the relation between the actual number of young born in a particular month which are raised to weaning age and the number of pairs of parents mated in the same month. The month referred to is the month in which the individuals were born and not the month in which 33 days of age was attained. The only modification involved is in the necessary correction for the days in the month which was made as for the litters per 100 matings. The effect of the corrections in the calculation of the indexes for per cent born alive and per cent raised of born alive can be determined

in any month by simply checking the young raised per 100 matings with the product of the litters per 100 matings, size of litter, per cent born alive, and per cent raised of born alive in the same month.

Effect of Litter Size and Sex on Weights, Gains, and Mortality.

Various investigators have indicated that the size of litter and sex have a distinct influence on birth weights, gains to weaning, and mortality. The proportion of large litters also differs in various seasons. It was, therefore, necessary in studying the influence of season on these characteristics to first determine the influence of litter size and sex, since an inaccurate elimination especially of the effect of size of litter might result in serious error.

The cards giving the record of each individual were sorted first according to sex, second according to size of litter, third according to month and year of birth, and fourth according to fate, i. e., those born dead (referred to as "borndead"), those dying between birth and weaning (referred to as "died"), and those which were raised to weaning at 33 days (referred to as "raised"). With this accomplished the groups of males and females born in each month of each year for each litter size were run through the tabulating machine and the numbers born dead and died with their birth weights and the number raised with their birth and weaning weights recorded. The number of litters born in each month was determined by the following formula:

$$\Sigma \frac{♂n + ♀n + ?n}{n}$$

in which ♂n, ♀n, and ?n denote respectively the number of males, females and individuals of unknown sex born in litters of n size and Σ

Table 1

Number of Litters and Individuals

Size of litter	Number of litters	Number of individuals	Number born alive	Number raised	Number[1] of males	Number[1] of females
1.....	2,037	2,037	1,650	1,351	1,008	1,001
2.....	3,952	7,904	6,854	5,759	3,970	3,854
3.....	3,693	11,079	9,442	7,892	5,538	5,405
4.....	1,641	6,564	5,074	4,070	3,261	3,209
5.....	484	2,420	1,710	1,333	1,202	1,179
6.....	116	696	431	303	353	332
7.....	19	133	79	52	67	63
8.....	3	24	17	15	15	9
Total of 1 to 6	11,923	30,700	25,161	20,708	15,332	14,980
Total of all	11,945	30,857	25,257	20,775	15,414	15,052

[1] Sex was not recorded for 391 individuals.

is the summation of numbers of litters of each size born in the month. By totaling and dividing by the number of individuals, the average birth weights of those born dead, died and raised, and the weaning weights and gains to weaning for the raised were determined for each sex and litter size in each month. The per cent born alive and per cent raised of those born alive were calculated from the numbers in each group for each sex and litter size. The totals for all months were used in evaluating the effect of sex and size of litter and were the basic data for the calculation of correction factors to eliminate the effect of size of litter and sex on weights and mortality in the calculation of the monthly indices.

The numbers of individuals in each size of litter are given in Table I as well as the numbers born alive and raised and the numbers of males and females. As may be observed in this table, the litter sizes in this stock varied from 1 to 8, averaging 2.583 $\pm$.0041 young per litter. The total number of individuals in each litter size was large except in litters of 7 and 8. The sex of 391 individuals was not determined when the original data were recorded, due to premature birth, partial eating of the young by the dam, or for other reasons. Such were necessarily eliminated from the calculations except in case of total numbers and litter sizes. The birth weights of 243 individuals were not recorded for various reasons. Their records were included in the numbers for sex and fate but obviously had to be eliminated in the calculations of weights. Chart I gives the percentage distribution of the population as litters and as individuals according to litter size. The solid line represents the

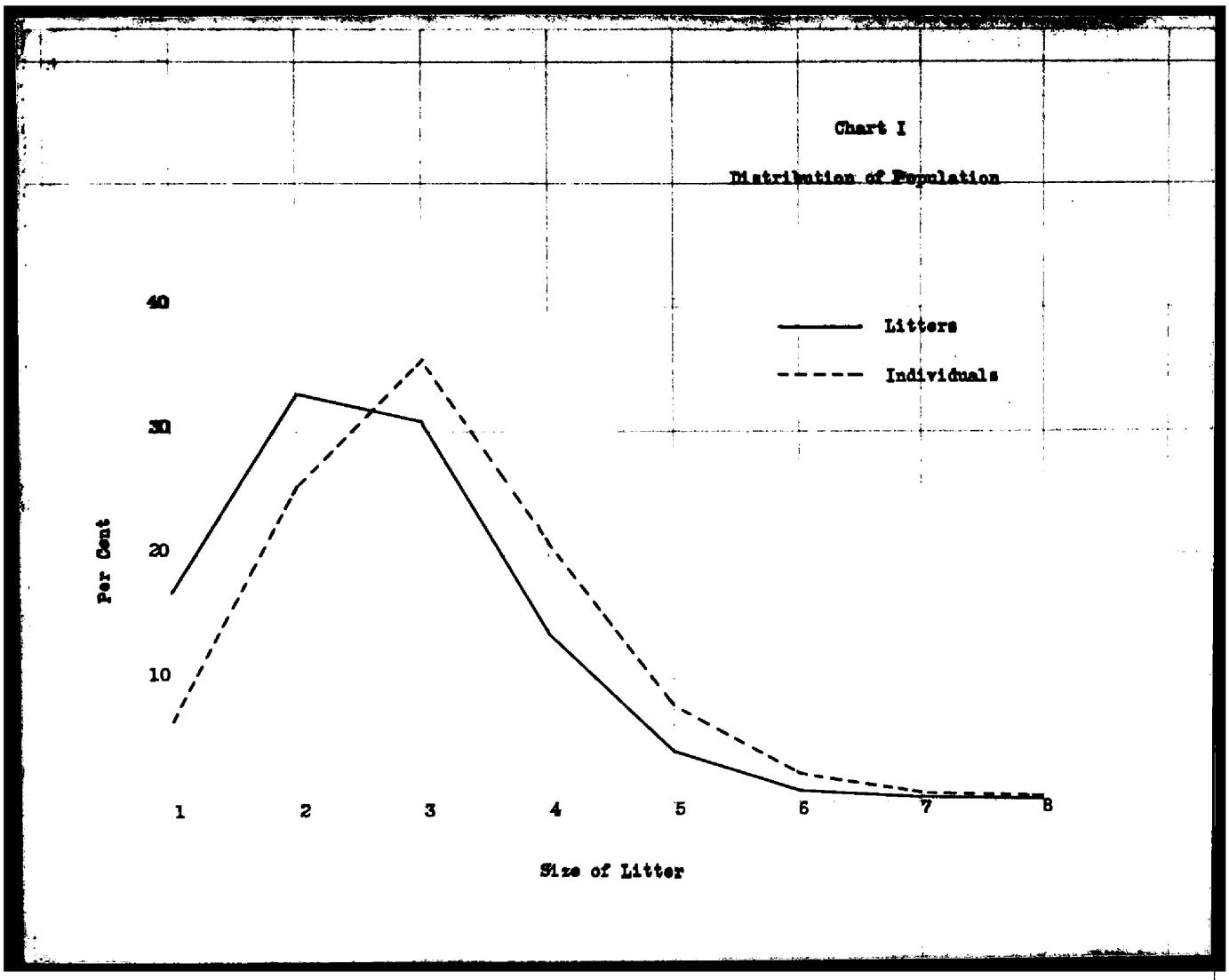


Chart I
Distribution of Population
Litters
Individuals
40
30
20
10
Per Cent
1
2
3
4
5
6
7
8
Size of Litter

percentages of the total litters made up of the litters of each size, and the broken line shows the proportion of the individuals which occur in the different sized litters. It is of interest that 82.79 per cent of the entire population was born in litters of 2, 3, and 4.

Because of the small numbers involved and their exceptional relations to the other litter sizes it was deemed advisable to eliminate individuals born in litters of 7 and 8 from the study of seasonal influences, but they are usually included in the tables giving averages according to litter size because of their possible interest and to make the data complete. Within the population, litters of 8 occurred at the rate of only 1 to nearly 4,000 litters, while there was only 1 litter of 7 for each 629 litters born. The large litters also came in the most favorable seasons. It thus seems reasonable to assume that litters of these two sizes are only produced with a most favorable complex of all related factors and then only by superior females. Their omission from the calculation of the monthly indices could have no significant influence on the final results.

Birth weights.- Wright (1922) pointed out that the birth weights of guinea pigs vary greatly, ranging from approximately 40 to 150 grams for those which are raised. He also mentions that size of litter is at least a very important contributory factor to the variability in weights and found a correlation of $-.658 \pm .007$ between size of litter and mean birth weight of litter mates. Minot (1891) also reported a decrease in birth weight associated with increased litter size in guinea pigs, as did Gates (1925) in mice and Kopec (1923) and Parkes (1926) in rabbits. Others have found like results in other animals. Table 2 giving the average birth weights of the individuals born in each litter size in the three groups of males

Table 2

Average Birth Weights

Litter size	Males			Females		
	Born dead	Died	Raised	Born dead	Died	Raised
	Grams	Grams	Grams	Grams	Grams	Grams
1	90.95	95.06	107.75	89.41	91.36	105.70
2	74.68	80.98	91.61	73.60	79.97	89.42
3	64.04	70.15	79.39	61.84	67.93	77.60
4	57.58	62.32	71.67	56.22	60.80	69.02
5	53.28	56.84	66.99	52.38	56.51	64.93
6	48.28	52.26	62.50	49.51	51.82	59.80
7	47.54	46.71	55.83	47.68	45.85	55.50
8	46.50	53.50	55.80	52.33	-----	64.50
Average of 1 to 6.	63.85	71.10	82.09	62.78	69.42	79.92
Average of all....	63.65	70.93	82.02	62.64	69.28	79.85

and females according to fate bears this out. Notwithstanding the extreme variability of individuals, Charts II and III show that the averages for those born dead, died or raised of each sex form relatively smooth and regular curves when plotted according to size of litter.

In all six groups the average birth weights of litters of 1 are decidedly the largest. A sharp downward trend in birth weights follows for litters of 2 and 3, but after this the weights decrease at a much slower rate. Litters of 7 and 8 show considerable irregularity, probably due to the small numbers.

The fate of the new born young within each size of litter appears to be closely associated with the average birth weight. In litters of 1 the males raised weigh nearly 13 grams and the females 14 grams more than those which die between birth and weaning. A difference of 8 to 10 grams is maintained throughout the different litter sizes in both sexes with small fluctuations, except for litters of 8. There is a smaller but quite consistent difference in the birth weights of those which are born alive but die before weaning and those which are born dead. . . The significance of the differences between the birth weights of those having different fates was tested for males and females according to Student's method, using litters of 1 to 6. Fisher (1928) p. 106. Table 3 gives the data needed for interpretation.

In calculating the standard deviation of the differences from the mean difference the formula, $\sigma = \sqrt{\frac{d^2}{n-1}}$ was used. With 6 litter sizes there are 5 degrees of freedom and from the table of t (Fisher 1928) if t = 4.032, P is .01. Since all values of t observed exceed 4.032

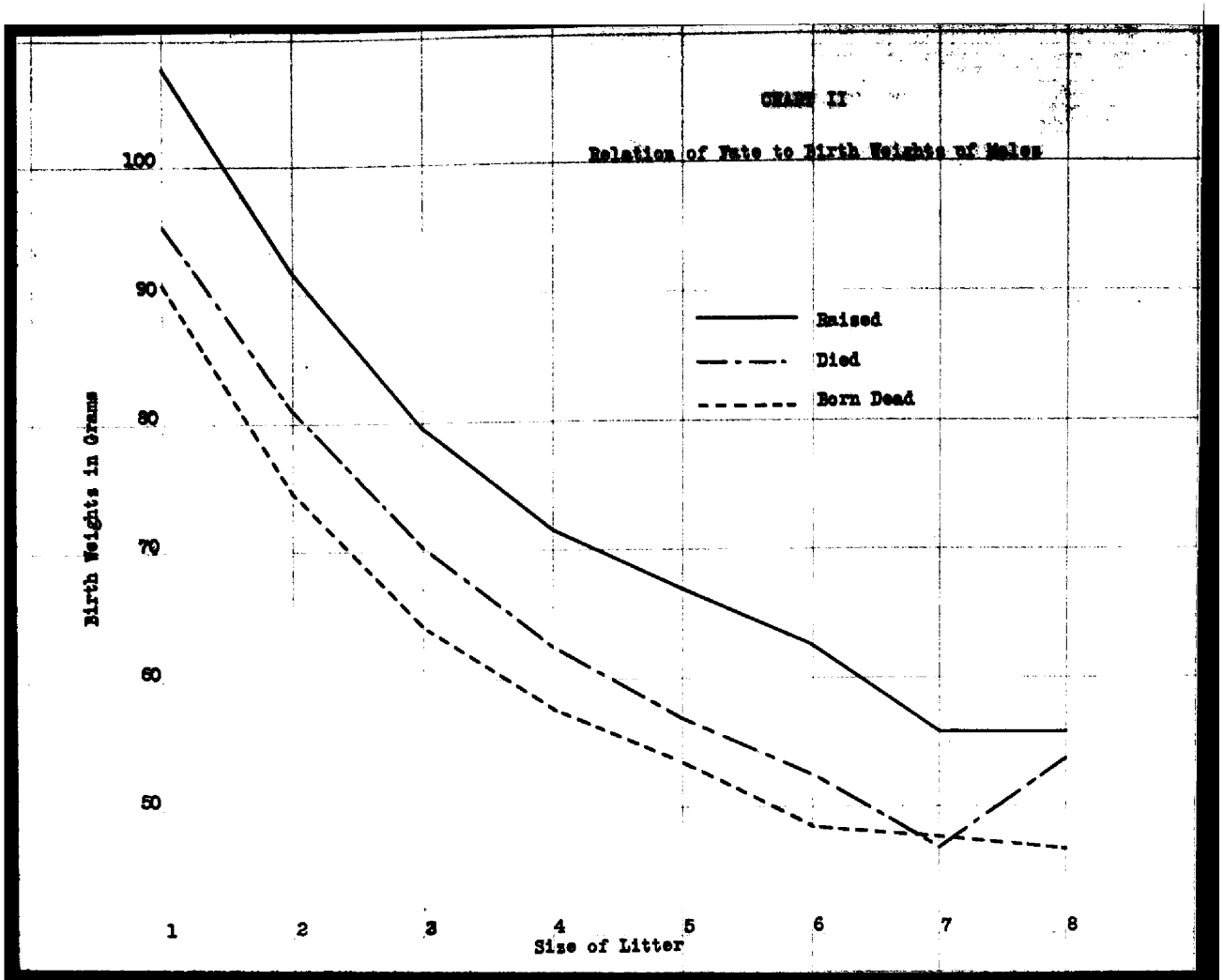


CHART II
Relation of Fate to Birth Weights of Males
Raised
Died
Born Dead
Birth Weights in Grams
100
90
80
70
60
50
1
2
3
4
5
6
7
8
Size of Litter

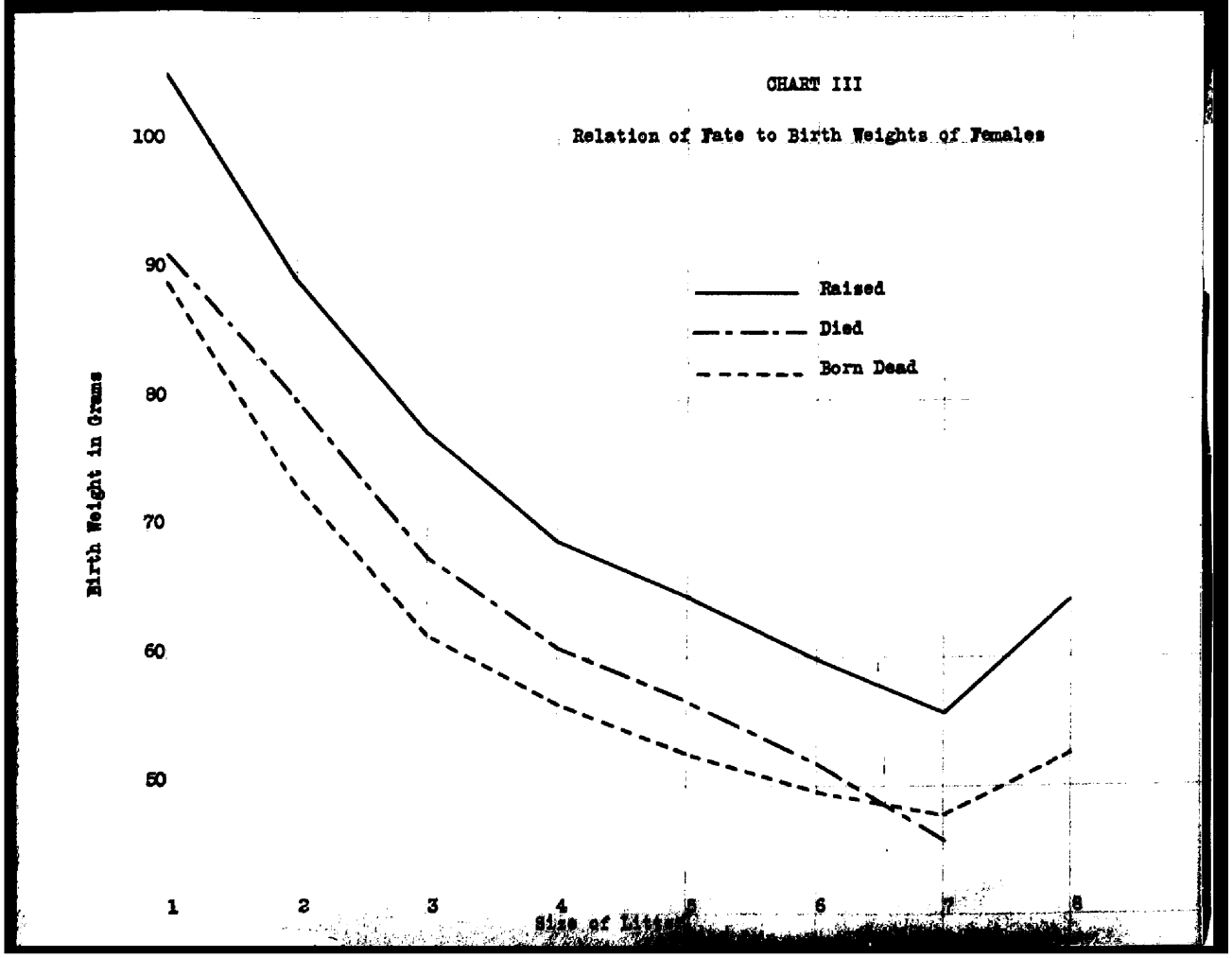


CHART III
Relation of Fate to Birth Weights of Females
Raised
Died
Born Dead
Birth Weight in Grams
100
90
80
70
60
50
1
2
3
4
6
7
8

Table 3

Comparison of Birth Weights According to Fate

Groups Compared	Mean Difference	Standard Deviation of Difference	t
	grams	grams	
Males born dead and died	4.80	1.154	10.19
Females born dead and died	4.24	1.847	5.63
Males died and raised	10.38	1.252	20,31
Females died and raised	9.68	2.382	9.96

there is less than one chance to ninety nine that the differences are not significant. It must, therefore, be concluded that the average birth weights of those having different fates differ significantly in both sexes, those raised being about 10 grams heavier than those dying between birth and weaning, and the latter group being about 4.5 grams heavier than those born dead.

It seems quite understandable that fate at birth and during weaning might be related to birth weights as the more immature and inherently weaker individuals as well as those resulting from unusually poor environmental conditions would naturally be more likely to succumb. But the average birth weight of 71.67 grams for males raised in litters of 4 is not as great as the average birth weights of those born dead in litters of 2 and is only slightly greater than the birth weights of those died in litters of 3. Such an outstanding effect of size of litter is indeed phenomenal. Expressed in another way the average birth weight which individuals born in litters of 1 must attain to be raised is more than 50 per cent greater than the average birth weight of those born dead in litters of 4. The average birth weight of those raised in litters of 4 is only about three fourths as heavy as those born dead in litters of 1. One would ordinarily think that weak individuals, and those light in weight are usually weak, would have a better chance of survival in a small litter than in a large litter, but the explanation must come from other sources, probably from the dam, agreeing with Wright's (1922) findings that birth weights and mortality at birth are largely maternal affairs. Differences between the mortality of the different sized litters are not sufficient for an explanation.

Slight differences in the shapes of the curves for those having different fates are apparent in both sexes, but the close approach to parallelism in the two sexes with the males slightly heavier in all groups and in nearly all litter sizes is beyond expectation. This is best noted in Charts IV, V, and VI. Because of the uniformity of the differences within different litter sizes males would appear to be heavier than females at birth, but the average differences between males and females in litters of 1 to 6 for those born dead was .98 grams and for those died 1.54 grams with respective standard deviations[1] of the differences of 1.170 and 1.272 grams respectively from which the values of t were calculated as 2.05 and 2.96. The corresponding P values were .1 and .04. Thus the sex difference in the birthweights of those born dead is not significant, and for those died it cannot be considered certain. The birth weights of males raised are also greater than the birth weights of females raised; the mean difference in litters of 1 to 6 was 2.24 grams with σ of .361 grams making t, 15.20 and P much less than .01. (With 5 degrees of freedom when t is 4.032, P equals .01). It may be concluded that birth weights are significantly related to size of litter, and fate before and after birth and the birth weights of those individuals which are raised, as well as those which die between birth and weaning, are related to sex.

[1] The standard deviation of the differences was calculated from the formula $\sigma = \sqrt{\frac{d^2}{n-1}}$

Chart IV

Birth Weights of Males and Females Born Dead

Males $y^{-1} = .008571 + .002592x - .000099x^2$
Females $y^{-1} = .008083 + .003255x - .000207x^2$

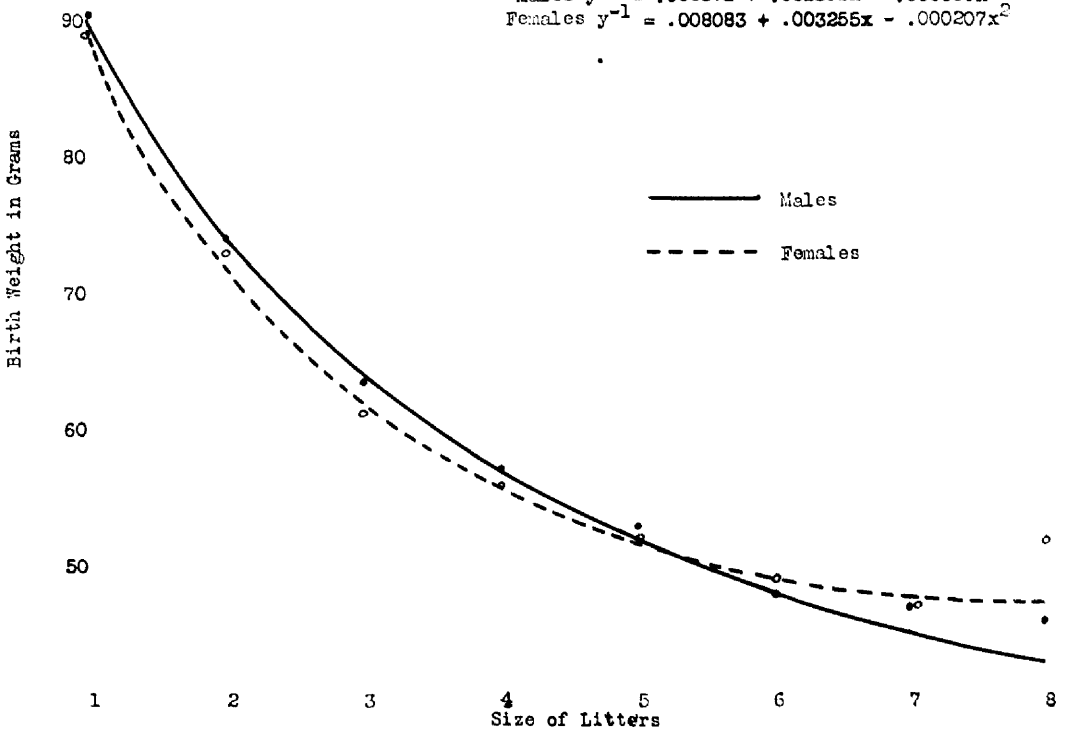
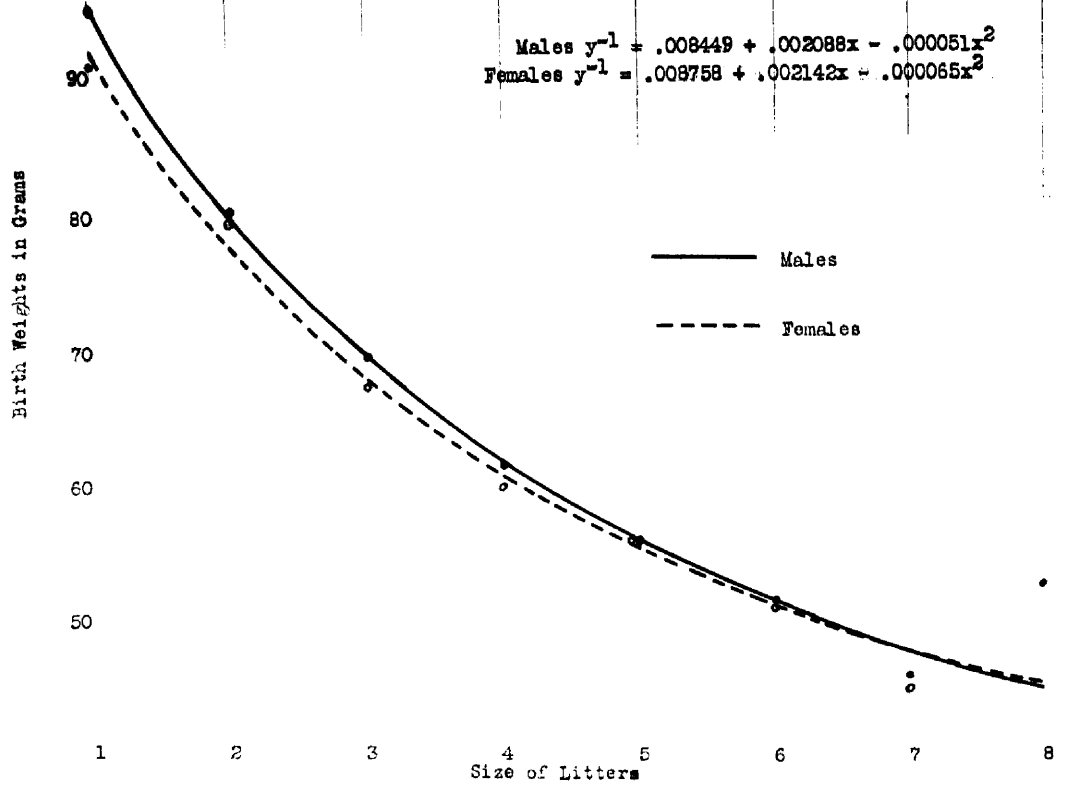


Chart V

Birth Weights of Males and Females Died

Males $y^{-1} = .008449 + .002088x - .000051x^2$
Females $y^{-1} = .008758 + .002142x - .000065x^2$



Weaning weight and gain. -- The effects of sex and size of litters on weaning weights and gains from birth to weaning are brought out in Table 4. Chart VII shows a pronounced effect of sex on weaning weight similar to that on birth weight. Males are heavier in all litter sizes. The relation of size of litter to weaning weight is also similar to its relation to birth weight, especially in the small litter sizes. The weaning weight curve takes the general course of the birth weight curves, but the drop is steeper for litters from 1 to 3, and the flattening is more pronounced for litters of from 4 to 6.

The mean difference between the weaning weights of males and females in litters of 1 to 6 was 8.62 grams and the standard deviation of the difference 2.731 grams; t was, therefore, 7.73 and with 5 degrees of freedom P is considerably less than .01.

The 33-day weight is a combination of the birth weight and the gain made between birth and weaning. Chart VIII shows the influence of sex and litter size on the gains between birth and weaning. Although it might be assumed that in an animal born as mature as the guinea pig and which is little dependent upon its dam's milk supply according to Ibsen (1922), the size of litter would have practically no effect on postnatal growth, it is very apparent that young born in the small litters have a distinct advantage in amount of gain whether due to the care and food supplied by the dam or their larger birth weights. Thus the larger average birth weights of the small litters and the greater gains made during the weaning period tend to make the curve showing the 33-day weights very steep at its origin. The percentage increase in weight during the weaning period (Table 4) is not directly related to birth weights but is inversely related. The increase for males in

$\sigma = \sqrt{\frac{\Sigma d^2}{n-1}}$

Table 4

Average Weaning Weights and Gains to Weaning.

Size of litter	Males			Females		
	Weaning weight	Gain		Weaning weight	Gain	
	Grams	Grams	Per cent of birth weight	Grams	Grams	Per cent of birth weight
1	280.18	172.43	160.03	273.79	168.09	159.03
2	251.17	159.56	174.17	241.26	151.84	169.81
3	221.23	141.84	178.66	215.40	137.80	177.58
4	204.12	132.45	184.81	196.64	127.62	184.90
5	198.87	131.88	196.87	190.02	125.09	192.65
6	192.56	130.06	208.10	179.30	119.50	199.83
7	201.38	145.55	260.70	178.71	123.21	222.00
8	145.40	89.60	160.57	141.00	76.50	118.60
Average of 1 to 6	228.22	146.13	178.01	220.48	140.56	175.88
Average of all	228.12	146.10	178.13	220.34	140.49	175.94

Chart VI

Birth Weights of Males and Females Raised

Males $y^{-1} = 0.007303 + 0.002050x - 0.000101x^2$
Females $y^{-1} = 0.007441 + 0.002089x - 0.000092x^2$

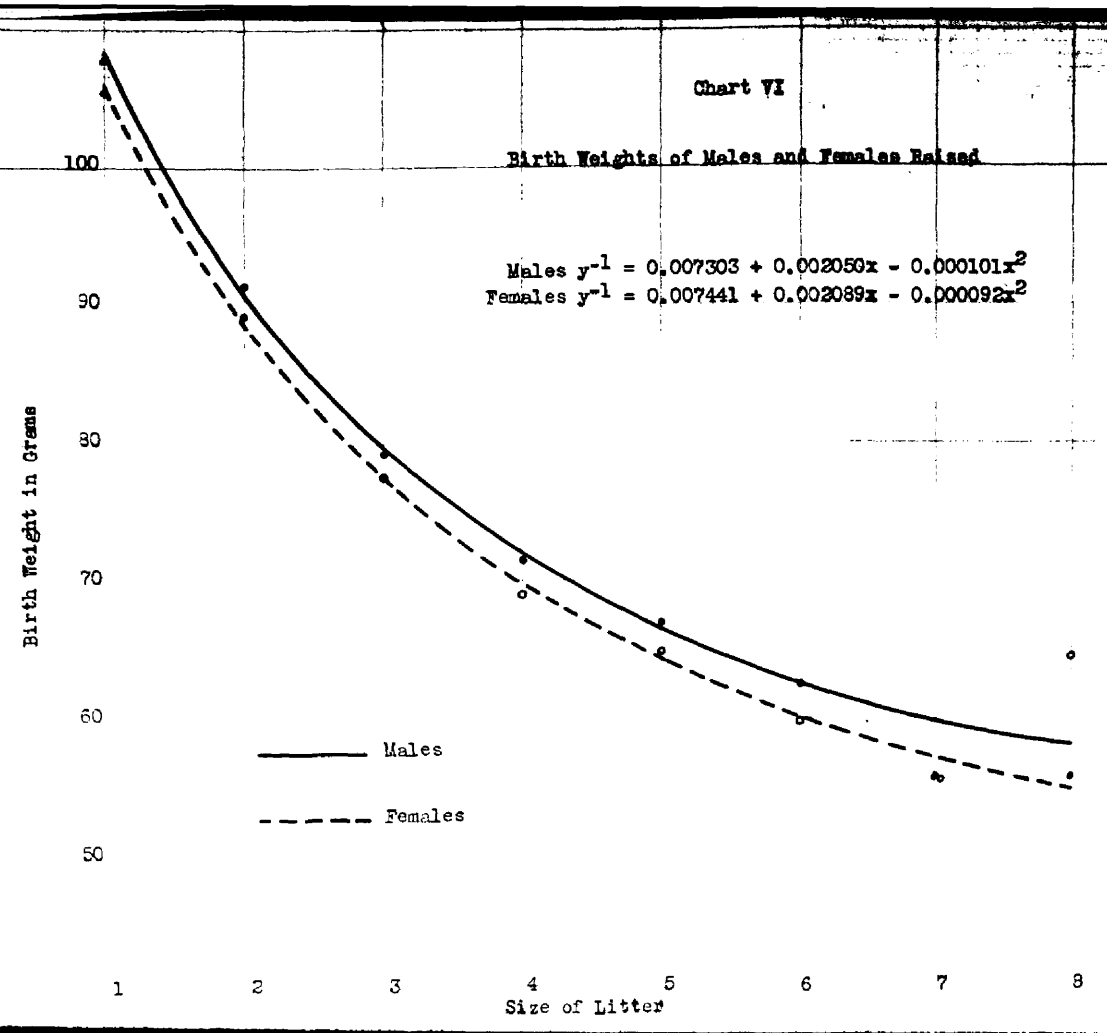


Chart VII

Weights of Males and Females at 33 Days

Males $y^{-1} = 0.0028884 + 0.0006922x - 0.0000514x^2$
Females $y^{-1} = 0.0030235 + 0.0006550x - 0.0000388x^2$

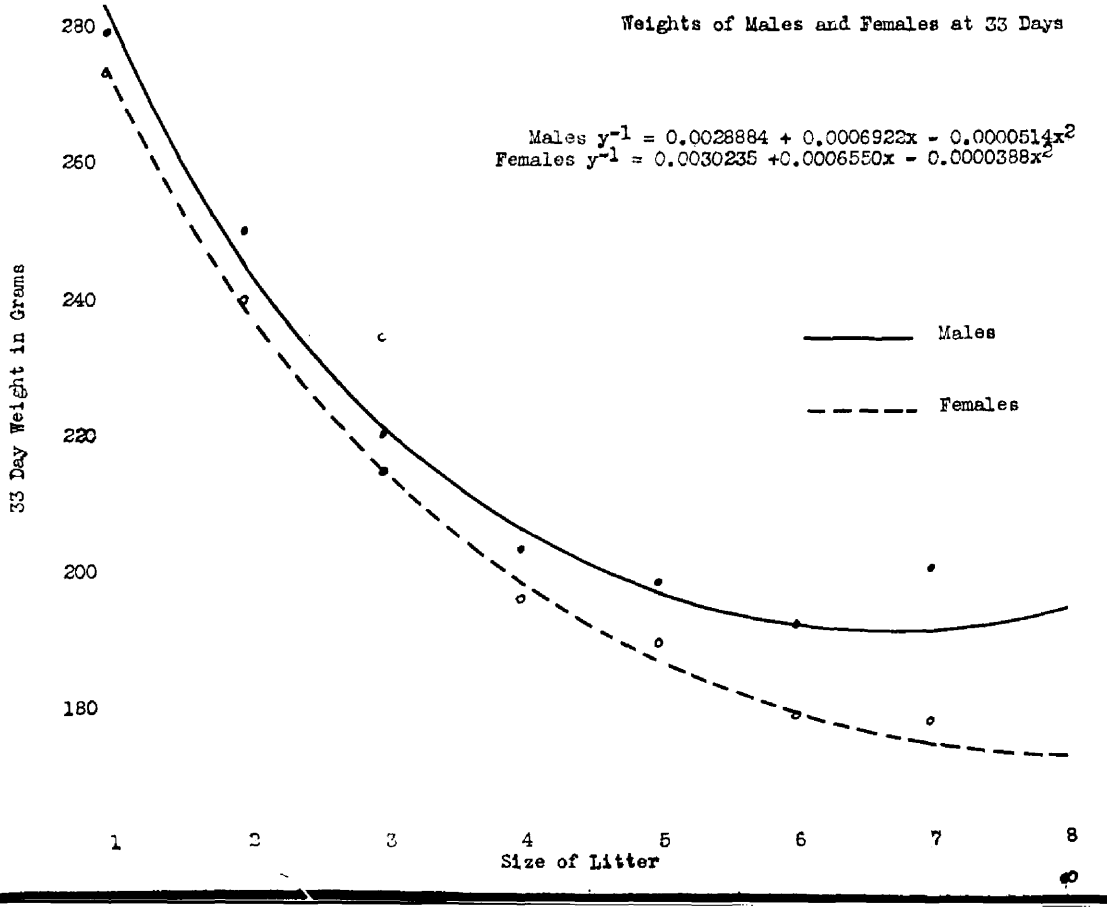


Chart VIII

Gains of Males and Females from Birth to Weaning

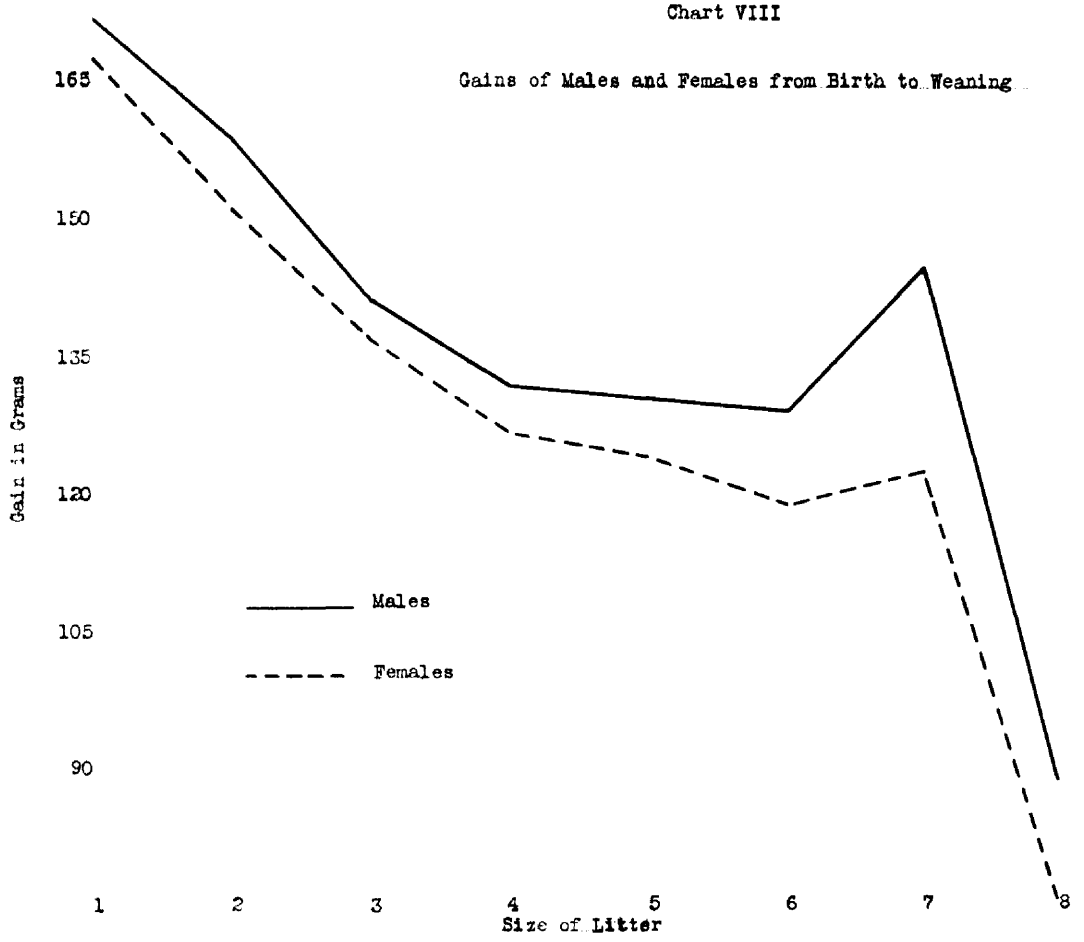
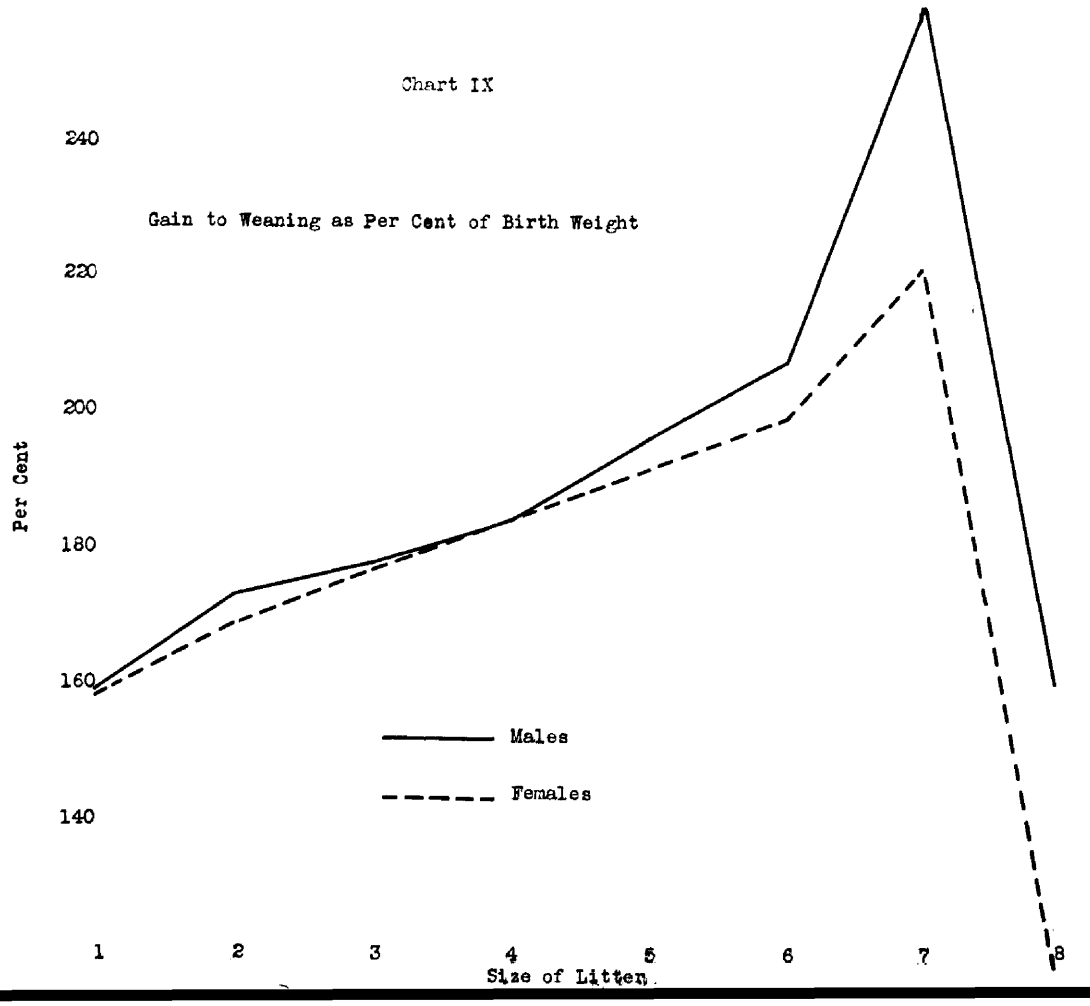


Chart IX

Gain to Weaning as Per Cent of Birth Weight



litters of 6 was calculated at 208.10 per cent, but in litters of 1 it was 160.03 per cent, with comparable values for females. Thus an increased relative gain accompanies an increase in litter size and tends to somewhat offset the percentage differences between the weights at birth in the different sized litters. Litters of 8 with the small numbers can hardly be considered as a reliable exception.

The mean differences between the gains of males and females in litters of 1 to 6 was 6.38 grams with a standard deviation of 2.509 grams, giving a value for t of 6.03; with 5 degrees of freedom P is, therefore, less than .01.

The weaning weights and gains between birth and weaning of males were thus significantly greater than those of females.

Fate of young:- -- A study of Table 5 giving the numbers born dead, died and raised of each sex born in litters of different sizes, shows that here again size of litter bears an important relationship. The percentages born alive and raised of those born alive are also plotted in Charts X and XI.

The one very striking feature of these data is that the chances for individuals born in litters of 1 to survive are less than for those born in litters of 2 and 3. It has been observed by Wright (1922) that frequently very large young are born dead, evidently due to difficulties at parturition, which might have some influence on the smaller per cent born alive in litters of 1, but this would in no way help to explain the lower per cent raised of those born alive in this

Table 5

Fate of Males and Females

Size of litter	Males					Females				
	Number born dead	Number died	Number raised	Per cent. born alive	Per cent. raised of born alive	Number born dead	Number died	Number raised	Per cent. born alive	Per cent. raised of born alive
1.....	173	145	690	82.84	82.63	186	154	661	81.42	81.10
2.....	503	533	2,934	87.33	84.63	467	562	2,825	87.88	83.41
3.....	715	772	4,051	87.09	83.99	786	778	3,841	85.46	83.16
4.....	737	473	2,051	77.40	81.26	659	531	2,019	79.46	79.18
5.....	332	190	680	72.38	78.16	339	187	653	71.25	77.74
6.....	142	61	150	59.77	71.09	112	67	153	66.27	69.55
7.....	29	14	24	56.72	63.16	22	13	28	65.08	68.29
8.....	4	2	9	73.33	81.82	3	--	6	66.67	100.00
Total of 1 to 6	2,602	2,174	10,556	83.03[1]	82.92[1]	2,549	2,279	10,152	82.98[1]	81.67[1]
Total of all	2,635	2,190	10,589	82.91[1]	82.86[1]	2,574	2,292	10,186	82.90[1]	81.63[1]

[1]Weighted average.

litter size. The explanation for the higher mortality in litters of 1 is probably due to the lowered vigor of dams producing litters as small as one. This bears out the importance of the influence of the dam on mortality not only before birth but during the weaning period. Young dams are probably in this group as well as dams low in vigor due to inherent weakness or unfavorable environment.

The chances of being born alive in litters of 4, 5 and 6 decrease very rapidly with each increase in litter size. It must be assumed that the dams producing the larger sized litters are relatively vigorous and the heavy mortality must be considered as a more direct effect of litter size on survival. The fact that the curve for per cent raised does not drop off nearly as rapidly with larger litters indicates the lesser dependence on the dam and is no doubt, also, a result of the reduced size of the larger litters through heavier mortality at birth.

Wright (1922) has pointed out that the most favorable litter size for mortality at birth and after birth varies according to the vigor of the stock. In the combination of the inbred families studied it was between litters of 2 and 3 for both percentages.

It is very apparent that there is less difference in mortality between the sexes than was found for the weights. The percentage born alive of the two sexes alternate at each litter size, indicating that there is no significant difference between males and females in this characteristic; the weighted averages were 83.03% for males and 82.98% for females, making a difference of .05% between the average values for the two sexes. There is a slight but constantly

Chart X

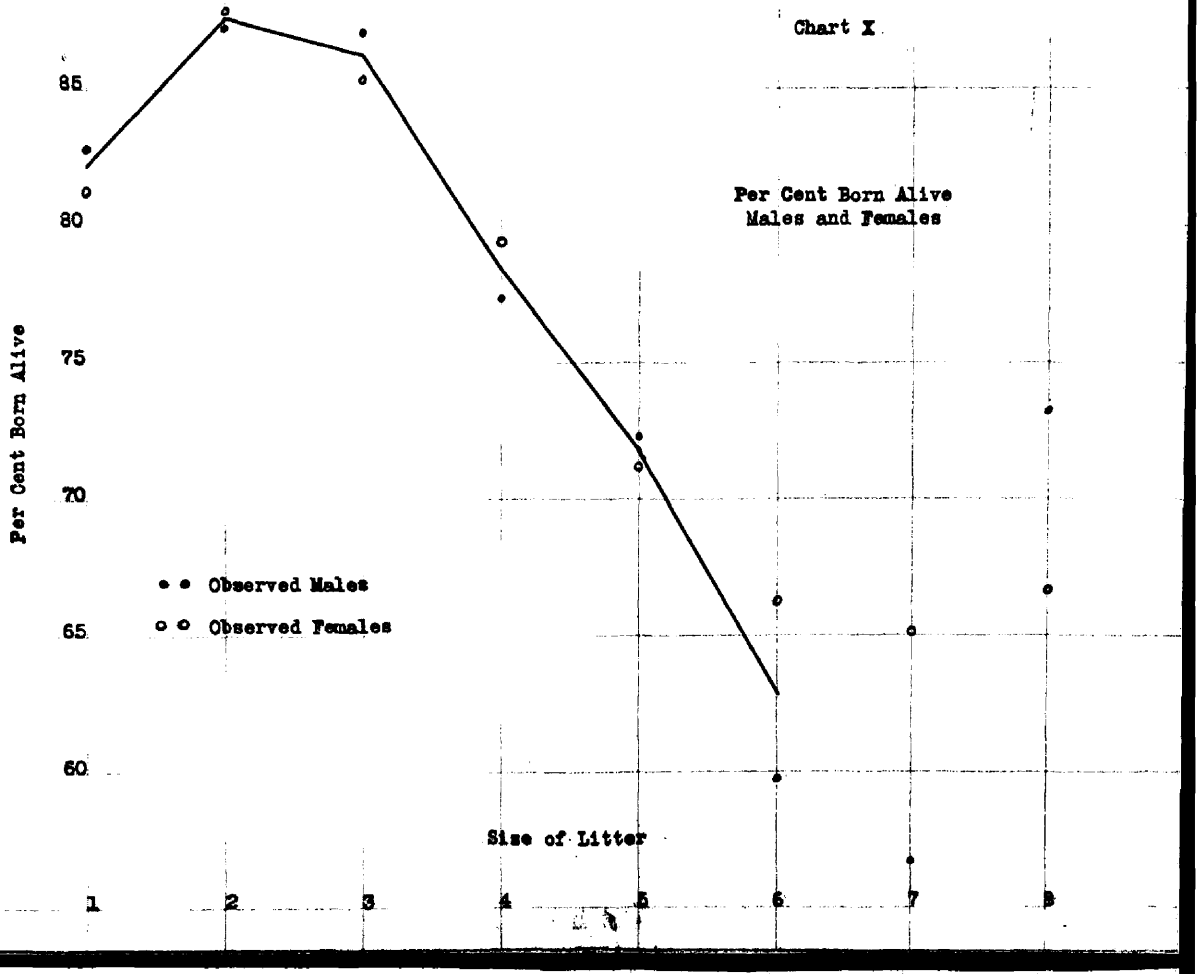
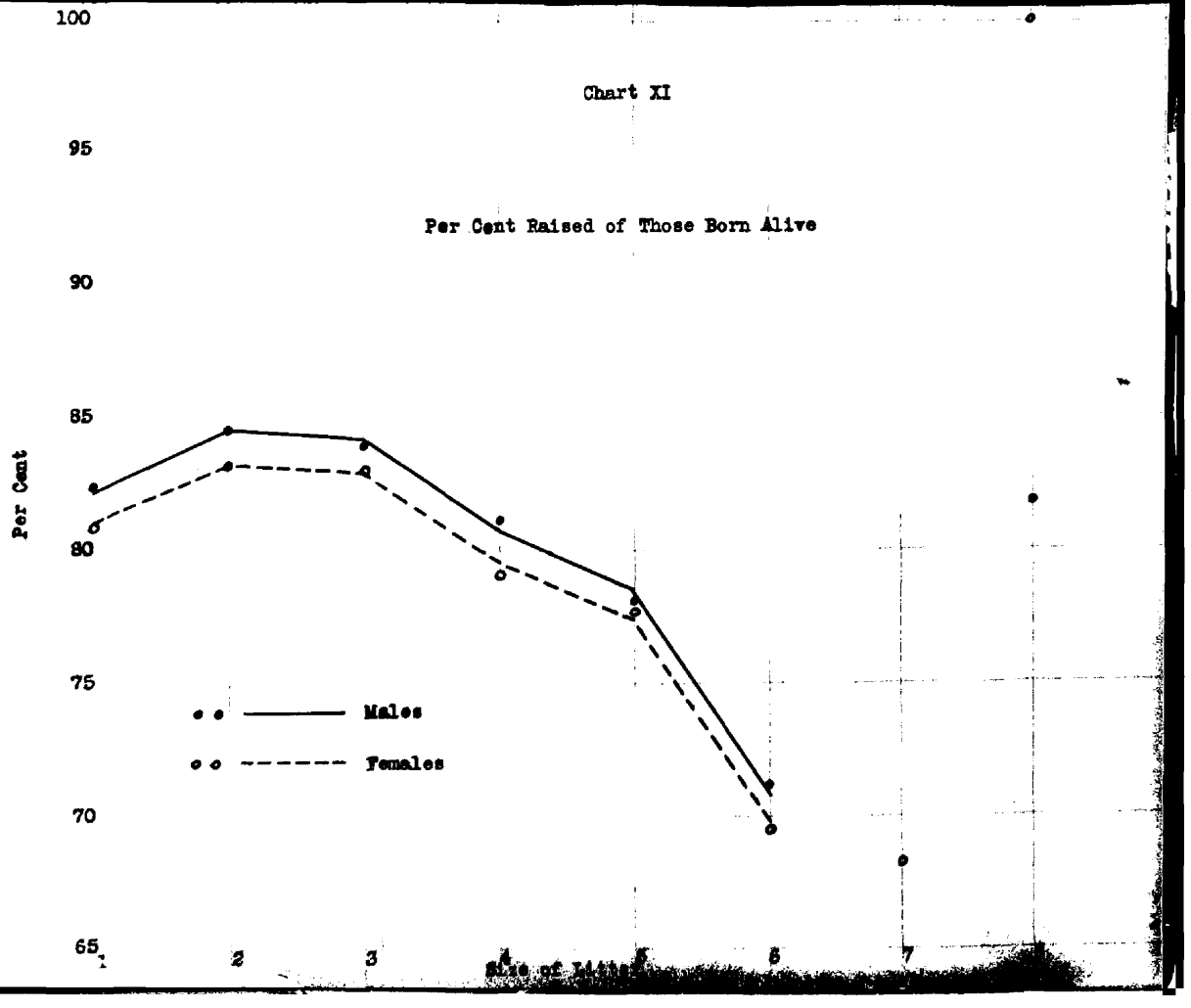


Chart XI



higher percentage of males than of females raised in litters of 1 to 6 (Chart X), the mean weighted averages being 82.92% for males and 81.67% for females. These curves differ materially from the curve of those born alive by indicating an effect of sex.

In an effort to test the likelihood of the distribution of males and females being within normal expectation chi - square was determined for four fold tables for each litter size from 1 to 6 according to the method outlined by Fisher (1925) using the formula:

$$X^2 = \frac{(ad - bc)^2 (a + b + c + d)}{(a + b)(c + d)(a + c)(b + d)} ,$$

in which a represents the number of males born dead, b the number of females born dead, c the number males born alive, and d the number of females born alive. The symbols represented similar values in the comparison of the sexes amongst those dying and born alive. The values of X^2 and P are given in Table 6. The X^2 values in litters of 3 and 4 indicated distributions of the sexes amongst the born dead and born alive which would occur less than 5 times in 100 if there were equal mortality of the 2 sexes. Since there were more males than females born alive in litters of 3, 87.09% males and 85.46% females and more females than males born alive in litters of 4, 79.46% females and 77.40% males, and because of the alternation of the 2 sexes in different litter sizes such cannot be considered as an indication of a difference in the mortality of the 2 sexes at birth even though the deviation from equality in the different litter sizes would be expected to occur

Table 6

Chi - Square Test of the Distribution of the Sexes According to Fate

Size of Litter	Born Dead and Born Alive		Died and Raised	
	X^2	P	X^2	P
1	.689	.30 to .50	.651	.30 to .50
2	.550	.30 to .50	1.898	.10 to .20
3	6.150	.01 to .02	1.204	.20 to .30
4	4.074	.02 to .05	3.469	.05 to .10
5	.377	.50 to .70	.045	.80 to .90
6	3.090	.05 to .10	.1231	.70 to .80
Total	14.931	.02 to .05	7.390	.20 to .30

but about twice in 100 times.

None of the X^2 values for the died and raised are without normal expectation with the possible exception of litters of 4 and this is not clearly significant.

Since males uniformly excel females in the percentages raised in litters of 1 to 6 Students Method affords a test for the significance of the difference. Comparison was therefore made of the percentages of males and females raised in litters of 1 to 6 and for completeness the percentages of the 2 sexes born alive was similarly treated. The mean difference in the percentage raised was 1.27% in favor of the males with a standard deviation of .586%. Thus t was 5.31 for which P with 5 degrees of freedom is less than .01. This difference is therefore clearly significant. The value of t obtained for the percentage born alive, .64 would be expected in about 5 to 6 out of 10 times if there were no difference.

The percentage males in the groups having different fates for those born in litters of 1 to 6 were, born dead 50.5145 ± .4701%, died 48.8210 ± .5052%, and raised 50.9755 ± .2341%. The difference between the per cent males amongst those born dead and died was 1.6935 ± .6901% and between those died and raised 2.1545 ± .5568%.

It must therefore be concluded that there is no significant difference between the sexes in the mortality at birth, but the mortality between birth and weaning is slightly but significantly heavier in females.

$\sigma = \sqrt{\frac{d^2}{n-1}}$

Probable error for per cent males equals $.6745 \sqrt{\frac{\%\sigma^{\prime} \times \%\,♀♀}{n}}$

The data presented show that the size of litter in which young are born bears an important relation to the fate at birth and between birth and weaning, litters of 2 and 3 being most favorable for survival. Sex had no influence on mortality at birth but the mortality of females was slightly greater than that of males between birth and weaning.

Sex Ratio.- There was 50.5941 ± .1929 per cent males amongst all young born, a probable significant departure from 50 per cent. The percentage of males in litters of 1, 2, 3, 4, 5, 6, 7, and 8 were 50.17, 50.74, 50.61, 50.42, 50.48, 51.53, 51.54, and 62.50 per cent respectively. These data give little support to the findings of Papanicolau (1921) of a high degree of fluctuation in the sex ratio in different litter sizes, nor do they show the high percentage of males (59%) in litters of 4, which were found in his stock. A higher percentage of males was found in litters of 6, 7, and 8, but sufficient litters all of the female sex and their complete elimination would not be expected to occur with the small numbers of litters of these sizes to account for the larger percentage of males. It would, however, appear that prenatal mortality in these large litters falls more heavily on females. Such would presuppose that litters of 6, 7, and 8 were larger at conception, which is questionable, tho not impossible. A higher primary sex ratio seems more logical. Data on the monthly variations in sex ratio also give some indication of a higher sex ratio when conditions are unfavorable, which might also be assumed to occur under the heavy competition in the large litters. The χ^2 test for the departure of the sex ratio in the different litter sizes (1 to 8) from the mean sex ratio does not give support to the significance of these values. X^2 was 2.0056. With $n = 7$, P is .96. Departures as great as these from the mean are thus to be expected, if there were no significance, 96 times in 100 trials.

The significance of the deviations from equality of the sexes was tested by Fisher's t method, using only litters of 1 to 6 in which the numbers are relatively large. The mean difference was 1.317% with a standard error of ±.3823, making t, 3.44 a value to be expected but about twice in 100 trials if there were no difference. If litters of 7 and 8 were included the probability would be less, and it must therefore be concluded that there is a significantly larger per cent of males than females in the stock at birth.

The sex ratio in the groups having different fates was noted above, and needs no further comments except to call attention to the slightly higher percentage of females in the group which died between birth and weaning.

Discussion of effect of size of litter and sex on weights and mortality.- References to related studies may be of interest in helping to explain how differences in the size of litter affect the characters considered. The two bulletins of Wright (1922) deal with an analysis of the effects of inbreeding from the same data up to 1920. The effects of litter size on the various characters were pointed out in those studies, but the analysis was not carried as far and no specific factors were suggested for use in correcting for this effec

The growth of male and female guinea pigs from birth to 30 days of age was reported by Read (1912). That work deals especially with the effect of weaning at different ages and the relative maturity at birth. Differences in the litter sizes were not considered. The same author (1912) determined the intrauterine growth cycles in the guinea pig by weighing 10 females at intervals during pregnancy. These data showed that the second growth cycle had started before birth as distinguished from other animals in which the second growth cycle is started after birth, Robertson (1923). Minot (1891) made a study of the growth

of guinea pigs from birth to maturity. The size of litter was found to have an important influence on birth weights, especially in the smaller litters. In this study the differences in the birth weights were mainly attributed to differences in the length of the gestation periods but Wright (1921) found that size of litter was much more effective in reducing birth weights by reducing the rate of growth than by causing early parturition. Differences in location or relation to other fetuses in the uterus may also influence the differences in the size of individuals in the same litter. Marshall (1922) has discussed the possible effects of limited nutrition of the dam, mainly with negative conclusions. Many others have called attention to the effects of litter size on birth weights including Parkes (1926) in mice, Hanson and Heys (1927) in the rat, Kopec (1923 and 1926) in the rabbit, Prawdchenski and Kaczkowski (1926) and Hansson (1927) in sheep and others. With the animals which are more mature at parturition and where the number in the litters are relatively small the effect of additional numbers is particularly important.

The birth weights, weaning weights and gains of the two sexes conformed with the general findings of others in most all classes of animals, males being generally heavier.

It is more difficult to suggest explanations for the effect of size of litter on mortality and especially postnatal mortality. The operation of lethal factors should be equally operative in all litter sizes and therefore cannot be considered. Nutrition might be a limiting factor provided the young became very much weakened from lack of food, which is quite likely a possible factor, as is indicated by the

similarity between the birth weights of those dying between birth and weaning and those dying at birth as contrasted with the considerable greater average weight of those raised, but the condition and age of the dam and maturity of the young seem to be likely possibilities. Here again the dam's influence particularly seems to be somewhat complicated. How can a female which is in good enough condition to produce a litter of 5, 6, or 7 be considered in too poor condition to raise as large a proportion of her young as a female producing a litter of 2 or 3? The explanation is possibly related to the maturity of the young at birth. Due to the greater mortality at birth in large litters the actual number which the dam has to care for are not so much greater than the number cared for in smaller litters. Maturity alone, however, cannot be the whole story as it is well known and has been pointed out by Minot (1891) and Wright (1922) that litters of 1 are most mature at birth, and yet both the percentages that are born dead and those which die between birth and weaning are larger in litters of 1 than in litters of 2 and 3. It may be that the explanation for the effect of litter size on mortality is a combination of the maturity and competition of the young and condition and age of the dam. The influence of the dam may particularly apply to litters of 1 whereas the maturity of the young is perhaps more important in large litters.

The sex ratios combined with mortality do not indicate large inequalities in the mortality of the two sexes at the different stages of development. The small differences during the weaning period were pointed out. Much has been published on the sex ratios of animals in

Table 7

Calculated Values of Constants in Parabola[1]

$$y^{-1} = a + bx + cx^2$$

Group	a	b	c
Birth weight of males born dead	0.008571	0.002592	-0.000099
Birth weight of females born dead	.008083	.003255	- .000207
Birth weight of males died	.008449	.002088	- .000051
Birth weight of females died	.008758	.002142	- .000065
Birth weight of males raised	.007303	.002050	- .000101
Birth weight of females raised	.007441	.002089	- .000092
Weaning weight of males	.0028884	.0006922	- .0000514
Weaning weight of females	.0030235	.0006550	- .0000388

[1](y is birth weight and x is size of litter).

many cases showing sex differences in mortality usually the male being less vigorous, but this study does not bear that out, females if anything being less viable during that period between birth and weaning. Crew (1924) and Parkes (1926) have summarized the normal sex ratios to be expected in various classes of animals.

Elimination of the Effect of Litter Size on Weights.

The primary purpose of determining the average weights of males and females born in the different sized litters was to get at some means of eliminating such effect in the calculation of monthly indices. The averages when plotted, especially in the litters from 1 to 6, formed relatively smooth curves. A very close fit to practically all the observations for birth weights and the 33-day weights were obtained for males and females having the different fates by fitting the formula $\underline{y^{-1}} = \underline{a} + \underline{b}\underline{x} + \underline{c}\underline{x^2}$ in which $\underline{y^{-1}}$ represents the reciprocal of the weight in any litter size, $\underline{x}$, from 1 to 6, and $\underline{a}$, $\underline{b}$, and $\underline{c}$ are constants. These values for males and females in the different groups are given in Table 7. The fitted curves for each group are shown in Charts 4, 5, 6, and 7. The solid line in each case represents the calculated curve for the weights of the males and the broken line the same for the females. Each observed average value is given as a solid dot for males and as a circle for females.

Correction factors for the weights of individuals born in any litter size were then calculated for each group from the formula $Cx = \frac{M}{Y}$, where $\underline{Cx}$ represents the correction factor for any litter size, $\underline{x}$, $\underline{m}$ is the mean weight of the group including all sized litters, and

y is the calculated average weight of the individuals born in a certain litter size, x. The reciprocals of the calculated weights for each litter size (y^{-1}) or so-called basic correction factors are given in Table 8. The actual correction factors calculated from these by multiplying by the mean of the group are given in Table 9.

It is possible that these correction factors might be applicable to other populations of guinea pigs for the elimination of the effects of litter size on weights at birth and weaning, provided that the time of weaning was comparable. In such a case it would probably be more appropriate to use the average weights of the stock studied if the corrected values were to be reduced to comparable weights for that stock. The correction factors were calculated from the averages for litters of 1 to 6, and the values for litters of 7 and 8 were determined by extrapolation, which is always uncertain and in certain of the cases here given obviously inaccurate, since in all cases the curves have a tendency to turn up at or near litters of 7 or 8, thus showing heavier weights for the individuals in larger litters, which is not at all in conformity with the general tendencies observed where the numbers are sufficient, though in certain cases the curves appear to fit the observed data more closely because of turning up. The curves should be considered as strictly discontinuous, the values only applying where x lies between 1 and 6, inclusive. Calculations for litters of 7 and 8 are given only for their possible interest in connection with the report but are not suggested for application, and litters of these sizes were eliminated from the calculation of monthly indices for weight and fate.

Table 9

Weight Correction Factors for Size of Litter

Group	Size of Litter					
	1	2	3	4	5	6
Birth weight of males born dead...	.706477	.853022	.986923	1.108181	1.216796	1.312768
Birth weight of females born dead.	.698815	.864180	1.003554	1.116937	1.204328	1.265728
Birth weight of males died.....	.745524	.883097	1.013418	1.136487	1.252304	1.360870
Birth weight of females died.....	.752141	.887297	1.013429	1.130537	1.238620	1.337679
Birth weight of males raised.....	.759529	.902946	1.029781	1.140032	1.233701	1.310787
Birth weight of females raised....	.754289	.899184	1.029375	1.144860	1.245639	1.331714
Weaning weight of males.....	.805426	.928220	1.027568	1.103468	1.155921	1.184928
Weaning weight of females.....	.802454	.921200	1.022841	1.107378	1.174810	1.225138

The corrected and uncorrected birth weights, weaning weights and gains to weaning derived in both ways for the combined months are given in Table 13 for an estimate of the effect, which it will be seen is not great, but they are doubtless effective in single months in which few litters are born.

Elimination of the Effect of Litter Size on Fate

The correction factors for the fates were not so easily smoothed as those for the weights. After a number of different methods and formulas had been tried, the most satisfactory method seemed to be to strike the midpoint between the values determined for males and females. The reciprocals for the combined percentages of males and females born alive multiplied by the average for all sized litters of 1 to 6 were used as the correction factors for percentage born alive. As no difference between the sexes was established, a single correction value was used for each litter size.

The basis for the correction factors for the effect of litter size on per cent raised was selected as the midpoint between the per cent males raised and the per cent females raised since there were nearly equal proportions of the two sexes amongst those raised. These points were then modified by the average of one-half the weighted difference between the males and females at each point, and thus parallel curves were constructed. This procedure was carried out only for litters of 1 to 6 and appeared quite satisfactory.

The correction factors based on the reciprocals of the smoothed values multiplied by the average for litters of 1 to 6 are given in Table 10 for the percentage of males and females born alive and raised.

An idea of the effect of the correction factors on mortality may be obtained from Table 12 where both corrected and uncorrected determinations for the per cent born alive and raised of born alive are given.

Seasonal Fluctuations in Monthly Indices.

All data were tabulated by months, litter size, fate and sex. After making proper correction for the birth weights and fates the corrected values were summed and the mean determined which was used as the index.

The monthly indices so calculated are presented in Table 11 and in Chart XII. The values for the indices are given in the right and left margins of the Chart, while the vertical lines represent the months from December 1906 to December 1924, inclusive. In considering any of the series of data the fact that the vigor of the stock was undergoing a slow but gradual decline throughout the period should not be overlooked. (Wright 1922). It is also of general interest in this connection that conditions were very favorable in 1910 and rather unfavorable for a period about 1915 to 1918.

Litters per 100 matings.- Dividing the time into calendar months has proven rather inappropriate for the calculation of this index as it gives a graph of a rather distinct zigzag or sawtooth character resulting from the fact that females producing litters in one month can not produce litters again in the next month due to the gestation period of 68 days. Evidently when conditions become favorable the reaction is pronounced and litters are produced by a large portion of

Table 11

Monthly Indices

Year	Month	Litters per 100 matings	Average size of litter	Per cent males	Average birth weight of those raised	Average gain to 33 days	Per cent born alive	Per cent raised of born alive	Young raised per 100 matings	Number of young born
					Grams	Grams				
1906	8	100.00	1.00	0.00	77.00	180.00	100.00	100.00	100.00	1
	9	41.67	3.40	52.94	81.58	154.17	102.88	71.12	100.00	17
	10	66.21	3.00	51.28	78.26	155.53	98.31	96.74	193.54	39
	11	-----	----	-----	-----	------	-----	-----	------	--
	12	21.50	2.67	50.00	98.87	120.73	98.06	93.13	53.77	16
1907	1	22.51	3.30	54.55	84.58	142.36	97.91	97.44	69.76	33
	2	33.16	2.00	53.85	74.14	141.05	92.31	82.72	53.57	26
	3	18.88	2.88	43.48	70.00	118.67	86.22	89.75	42.48	23
	4	20.45	2.33	52.38	68.36	138.50	68.38	91.73	31.82	21
	5	25.57	2.50	48.57	85.03	180.45	97.23	93.31	60.25	35
	6	33.90	2.45	51.02	83.90	172.22	90.43	90.60	69.49	49
	7	30.79	3.24	47.06	79.82	153.90	103.24	96.94	89.43	68
	8	38.71	3.14	47.73	81.25	141.24	97.02	95.78	106.45	88
	9	28.09	2.60	52.31	77.49	147.36	91.86	95.37	59.55	65
	10	27.10	2.82	53.16	78.00	162.10	78.34	95.70	56.13	79
	11	33.03	2.97	52.34	81.53	150.65	93.20	89.00	80.73	107
	12	26.00	2.53	48.19	76.97	142.43	85.99	90.82	48.39	91
1908	1	14.99	2.18	41.67	72.70	131.60	75.65	77.58	20.45	48
	2	25.53	2.59	46.53	78.74	123.90	77.71	74.26	39.94	101
	3	29.03	2.44	52.21	75.68	115.51	68.03	78.91	37.50	117
	4	23.84	2.06	52.86	80.00	171.08	76.19	97.04	35.76	74
	5	33.66	2.33	43.12	87.16	197.74	84.35	96.35	63.11	112
	6	32.35	2.61	44.35	90.17	174.51	95.48	95.75	76.47	115
	7	35.13	3.13	45.18	86.40	164.86	94.59	96.89	95.44	166
	8	28.86	3.33	52.35	83.94	165.82	93.10	95.76	78.66	170
	9	21.69	2.76	56.64	84.04	150.93	79.16	88.53	40.21	113
	10	35.15	2.94	46.55	87.27	153.73	93.02	95.00	84.19	238
	11	24.43	2.97	47.89	81.10	144.95	90.86	94.15	59.16	190
	12	28.21	3.04	48.36	78.31	116.20	89.99	82.10	58.37	219

Table 11 Cont.

Monthly Indices

Year	Month	Litters per 100 matings	Average size of litter	Per cent males	Average birth weight of those raised	Average gain to 33 days	Per cent born alive	Per cent raised of born alive	Young raised per 100 matings	Number of young born
					Grams	Grams				
1909	1	29.81	2.69	50.66	76.79	114.56	79.58	66.09	42.42	229
	2	17.42	2.32	53.85	72.18	86.71	78.31	56.22	17.42	109
	3	33.84	2.21	54.68	71.60	103.52	67.29	55.94	26.73	221
	4	25.27	2.46	56.07	72.08	123.60	78.19	84.68	42.35	175
	5	18.23	2.50	47.29	73.67	156.16	79.40	87.11	31.56	130
	6	42.96	2.62	50.32	83.83	163.21	94.66	96.59	101.81	312
	7	24.56	2.85	51.08	82.92	160.91	99.34	93.37	61.04	188
	8	31.79	3.32	48.34	82.03	155.35	90.24	91.44	79.30	302
	9	26.52	2.80	52.31	85.14	177.03	92.32	94.59	64.02	196
	10	31.99	2.80	51.98	88.98	178.83	89.75	98.41	77.02	227
	11	27.21	2.69	54.87	91.31	161.61	90.21	95.09	61.03	199
	12	34.66	2.87	54.33	83.57	171.93	87.96	88.88	75.49	290
1910	1	32.91	2.88	54.58	82.52	171.22	89.95	93.36	77.02	288
	2	30.22	2.94	50.00	80.50	151.02	90.75	95.17	74.61	232
	3	35.72	3.22	50.14	78.15	158.49	89.55	89.13	84.56	377
	4	25.82	3.29	45.10	82.76	187.52	93.14	95.33	70.92	286
	5	34.96	2.87	50.14	88.85	196.68	93.36	89.27	80.83	359
	6	34.68	2.88	51.75	87.07	189.24	90.04	95.37	82.80	371
	7	29.99	3.25	48.60	86.74	160.84	95.71	95.27	82.32	357
	8	33.88	3.04	48.68	84.54	150.71	91.34	91.21	82.13	380
	9	26.61	2.84	51.84	83.06	162.44	87.88	86.82	56.27	247
	10	29.54	2.85	51.61	89.16	164.46	86.69	93.43	65.42	279
	11	30.16	3.06	43.99	86.89	135.65	87.11	91.43	70.16	291
	12	39.53	2.90	51.79	83.22	133.70	79.58	85.29	75.90	363
1911	1	27.60	2.49	52.07	79.00	138.43	74.00	81.05	42.20	217
	2	18.60	2.30	52.03	82.07	119.70	81.99	71.93	25.84	124
	3	25.83	2.44	49.29	80.37	126.34	75.20	78.97	37.99	212
	4	30.50	2.52	49.18	79.99	147.97	78.21	86.76	53.46	244
	5	26.33	2.41	49.00	85.45	182.58	83.49	88.45	47.27	200
	6	25.99	2.51	48.99	84.94	157.22	87.30	88.01	49.67	198
	7	30.66	2.92	54.29	83.77	139.10	83.59	91.22	67.39	280
	8	27.13	2.68	46.06	83.34	125.22	83.82	81.83	48.84	241
	9	17.13	2.24	55.96	75.39	105.64	73.10	76.09	21.68	110
	10	22.62	2.44	51.15	81.17	126.22	63.37	73.62	25.76	176
	11	23.05	2.57	46.32	81.28	138.50	87.55	87.60	46.42	190
	12	24.78	2.19	53.13	81.28	125.50	81.17	91.68	41.77	160

Table11 Cont.

Monthly Indices

Year	Month	Litters per 100 matings	Average size of litter	Per cent males	Average birth weight of those raised	Average gain to 33 days	Per cent born alive	Per cent raised of born alive	Young raised per 100 matings	Number of young born
					Grams	Grams				
1912	1	35.22	2.62	49.58	82.84	134.59	83.05	84.99	66.19	238
	2	19.75	2.37	44.95	80.94	145.17	84.53	78.60	30.48	109
	3	24.80	2.36	49.31	81.81	154.04	84.34	78.67	39.44	144
	4	31.65	2.57	44.04	87.72	161.08	85.63	79.83	56.54	193
	5	22.72	2.33	50.79	88.83	149.58	89.83	89.32	42.92	126
	6	32.42	2.90	52.91	81.56	158.45	85.80	90.34	70.78	206
	7	28.60	2.79	49.51	84.87	158.62	85.38	92.08	62.29	204
	8	28.61	2.84	50.46	83.26	149.57	96.02	83.31	63.26	216
	9	26.09	2.60	47.59	81.81	147.17	87.49	92.66	54.71	187
	10	28.55	2.71	59.01	82.54	138.78	87.90	80.88	54.65	222
	11	27.61	2.78	51.32	78.17	138.20	73.62	78.36	44.78	228
	12	23.84	2.45	47.93	77.80	116.69	72.62	74.57	32.49	169
1913	1	17.28	2.48	54.84	76.73	105.17	74.06	51.53	16.93	124
	2	30.06	2.27	51.41	79.49	103.66	78.27	59.74	32.76	177
	3	20.76	2.37	51.43	78.07	146.85	78.16	66.98	26.75	140
	4	15.97	2.19	51.09	84.31	150.97	88.10	86.09	27.00	92
	5	24.77	2.30	49.66	84.89	171.39	89.20	94.72	48.00	147
	6	37.20	2.77	53.88	85.26	174.61	88.85	92.29	83.60	258
	7	22.31	2.73	49.67	84.05	184.45	95.88	91.73	51.38	153
	8	34.45	2.82	49.80	80.52	166.08	85.80	91.33	73.93	251
	9	21.00	2.44	52.08	82.48	162.00	89.76	87.55	40.57	144
	10	25.41	2.41	52.13	84.53	129.74	87.26	81.52	43.98	188
	11	26.75	2.31	51.30	80.29	95.61	85.62	56.20	30.57	194
	12	23.40	2.30	53.29	83.60	101.92	67.86	44.68	17.01	152
1914	1	17.23	2.19	54.35	80.68	150.60	79.78	71.34	21.73	92
	2	20.12	1.98	54.12	83.93	162.70	71.38	89.19	26.67	85
	3	31.41	2.35	51.72	86.41	170.51	80.33	73.87	44.99	174
	4	21.33	2.35	48.67	83.06	156.79	95.06	89.86	42.67	113
	5	29.59	2.57	48.15	88.16	180.60	86.83	88.47	58.72	162
	6	22.69	2.59	49.61	84.92	167.26	92.94	89.97	49.07	127
	7	29.50	3.00	45.83	82.25	151.72	91.89	88.87	65.44	192
	8	28.78	2.70	45.70	79.88	165.30	84.42	86.48	57.14	186
	9	19.15	2.62	51.69	83.60	165.02	74.47	85.85	32.77	118
	10	23.99	2.58	45.16	85.93	158.70	92.48	86.58	49.19	155
	11	34.36	2.74	47.95	84.13	135.19	88.61	92.15	76.06	244
	12	24.28	2.76	48.65	81.91	130.78	85.62	86.14	49.65	185

Table11 Cont.

Monthly Indices

Year	Month	Litters per 100 matings	Average size of litter	Per cent males	Average birth weight of those raised	Average gain to 33 days	Per cent born alive	Per cent raised of born alive	Young raised per 100 matings	Number of young born
					Grams	Grams				
1915	1	23.16	2.39	53.75	83.06	146.44	80.18	82.42	37.67	160
	2	19.51	2.17	56.52	82.03	129.62	70.90	71.69	22.09	115
	3	29.27	2.36	52.24	79.27	134.18	83.02	73.99	44.08	201
	4	18.77	2.49	45.08	77.60	135.10	82.78	76.94	30.65	122
	5	20.37	2.60	57.04	83.88	121.42	80.96	88.68	38.79	135
	6	26.62	2.56	50.28	77.25	135.89	89.00	87.17	53.23	179
	7	29.47	2.69	52.29	79.36	146.15	86.47	83.56	56.39	218
	8	25.50	2.74	50.50	78.97	122.67	90.81	86.67	55.55	200
	9	30.21	2.61	52.86	74.60	124.38	82.10	87.55	56.94	227
	10	27.07	2.74	52.94	78.64	128.54	75.40	83.64	47.29	238
	11	28.62	2.43	49.07	77.55	119.24	82.05	83.84	48.87	216
	12	21.38	2.17	49.36	75.41	109.60	82.16	84.12	32.95	156
1916	1	27.52	2.35	51.63	70.62	104.06	70.07	60.43	28.11	219
	2	23.35	2.29	51.88	77.73	106.02	61.46	43.01	14.27	165
	3	23.64	2.17	58.60	74.03	100.27	59.43	30.45	9.45	163
	4	22.81	2.17	44.27	73.23	102.40	57.06	51.18	14.04	141
	5	16.44	2.16	47.37	74.13	131.14	71.70	73.13	19.43	95
	6	25.00	2.31	47.62	73.81	95.02	88.32	84.91	44.14	148
	7	29.75	2.48	46.35	68.92	89.52	84.79	84.78	53.47	196
	8	28.99	2.64	47.72	67.04	96.52	72.30	65.77	35.02	203
	9	19.92	2.23	53.40	70.43	110.81	66.42	64.81	19.49	105
	10	25.60	2.44	46.45	75.35	109.27	71.00	68.98	31.19	156
	11	27.50	2.41	54.72	73.57	99.21	83.60	72.88	41.67	159
	12	18.95	2.23	53.85	67.19	54.50	70.95	23.51	6.45	105
1917	1	24.50	2.07	53.78	64.83	110.37	63.95	43.61	14.29	124
	2	11.85	1.88	52.17	74.27	103.00	59.04	53.18	7.11	47
	3	27.50	2.37	48.39	69.38	101.62	77.06	51.72	26.49	128
	4	23.84	2.32	52.75	64.47	88.61	61.64	61.28	20.93	95
	5	18.63	2.23	48.44	67.59	114.73	73.63	76.29	22.24	69
	6	29.45	2.02	55.32	71.80	97.41	78.18	85.68	40.49	97
	7	23.27	2.34	51.76	64.23	120.17	83.91	81.52	36.74	89
	8	24.79	2.19	57.58	67.69	104.48	78.52	65.38	28.00	68
	9	24.39	2.20	47.54	70.17	124.88	89.11	74.18	34.15	66
	10	30.90	2.37	56.67	70.70	139.96	76.37	70.76	40.66	90
	11	20.54	2.35	40.74	74.68	133.66	91.15	87.50	39.29	54
	12	37.08	2.15	40.70	75.73	122.86	78.64	78.97	50.65	88

Table 11 Cont.

Monthly Indices

Year	Month	Litters per 100 matings	Average size of litter	Per cent males	Average birth weight of those raised	Average gain to 33 days	Per cent born alive	Per cent raised of born alive	Young raised per 100 matings	Number of young born
					Grams	Grams				
1918	1	26.48	1.93	38.00	72.60	124.69	88.34	77.00	31.95	56
	2	24.89	2.39	49.06	69.42	111.61	85.89	71.20	35.71	55
	3	29.78	2.41	48.65	67.14	107.83	80.00	56.79	32.56	77
	4	26.17	2.39	49.23	66.56	85.16	69.25	38.65	16.82	67
	5	21.61	2.35	58.49	64.19	77.95	56.91	66.94	19.73	54
	6	20.00	2.10	56.41	70.04	98.54	77.23	76.61	24.00	42
	7	32.58	2.30	58.90	71.19	91.28	84.04	73.90	46.41	76
	8	29.54	2.52	49.30	63.14	106.68	79.15	48.81	28.52	73
	9	19.05	1.81	51.85	71.27	138.73	78.04	67.14	17.86	29
	10	19.75	2.30	52.38	82.20	167.43	91.88	89.51	34.56	46
	11	21.57	2.27	48.94	81.83	165.05	90.64	95.07	40.20	50
	12	29.57	2.36	48.72	80.37	168.23	84.96	95.58	60.04	78
1919	1	28.70	2.47	59.43	81.28	152.67	64.77	89.04	42.71	106
	2	18.50	2.84	57.41	77.55	127.19	91.26	77.71	37.02	54
	3	34.67	2.30	53.06	82.38	140.24	77.10	83.51	53.22	99
	4	20.16	2.60	55.38	83.77	158.40	82.55	86.63	37.90	65
	5	35.41	2.44	52.73	78.15	129.21	89.38	87.48	69.23	110
	6	31.50	2.50	50.00	80.47	138.45	80.16	68.29	41.73	100
	7	31.19	2.59	40.59	79.42	135.50	85.69	74.12	51.18	101
	8	27.10	2.51	55.17	74.85	120.50	73.00	82.22	41.80	88
	9	27.91	2.61	56.99	76.99	113.11	78.25	92.58	53.49	94
	10	28.07	2.39	48.89	76.09	114.78	71.98	82.65	40.62	91
	11	23.31	2.58	44.30	70.57	106.79	87.06	76.70	39.85	80
	12	26.81	2.12	55.81	76.07	126.95	83.63	78.64	39.23	87
1920	1	22.73	2.40	54.88	77.53	127.00	77.49	88.42	37.67	84
	2	33.59	2.24	49.07	76.87	127.02	86.70	81.40	53.07	112
	3	26.51	2.35	58.00	74.57	116.11	87.80	70.25	38.83	101
	4	23.38	2.47	45.98	76.18	123.74	75.41	78.39	34.42	89
	5	23.75	2.38	54.26	73.31	137.04	85.82	86.98	42.74	95
	6	31.88	2.33	45.69	74.02	138.90	72.55	74.84	41.25	119
	7	30.66	2.37	43.33	74.28	156.93	92.41	83.33	56.50	121
	8	31.66	2.89	52.29	76.44	155.68	82.07	87.85	63.92	153
	9	31.29	2.51	50.78	81.79	163.85	89.55	92.91	65.64	128
	10	28.85	2.60	46.28	83.24	151.68	81.91	85.73	51.69	125
	11	27.49	2.60	50.00	81.61	129.00	87.11	84.31	53.80	122
	12	35.34	2.77	46.93	74.43	120.95	70.85	74.43	52.73	180

Table11 Cont.

Monthly Indices

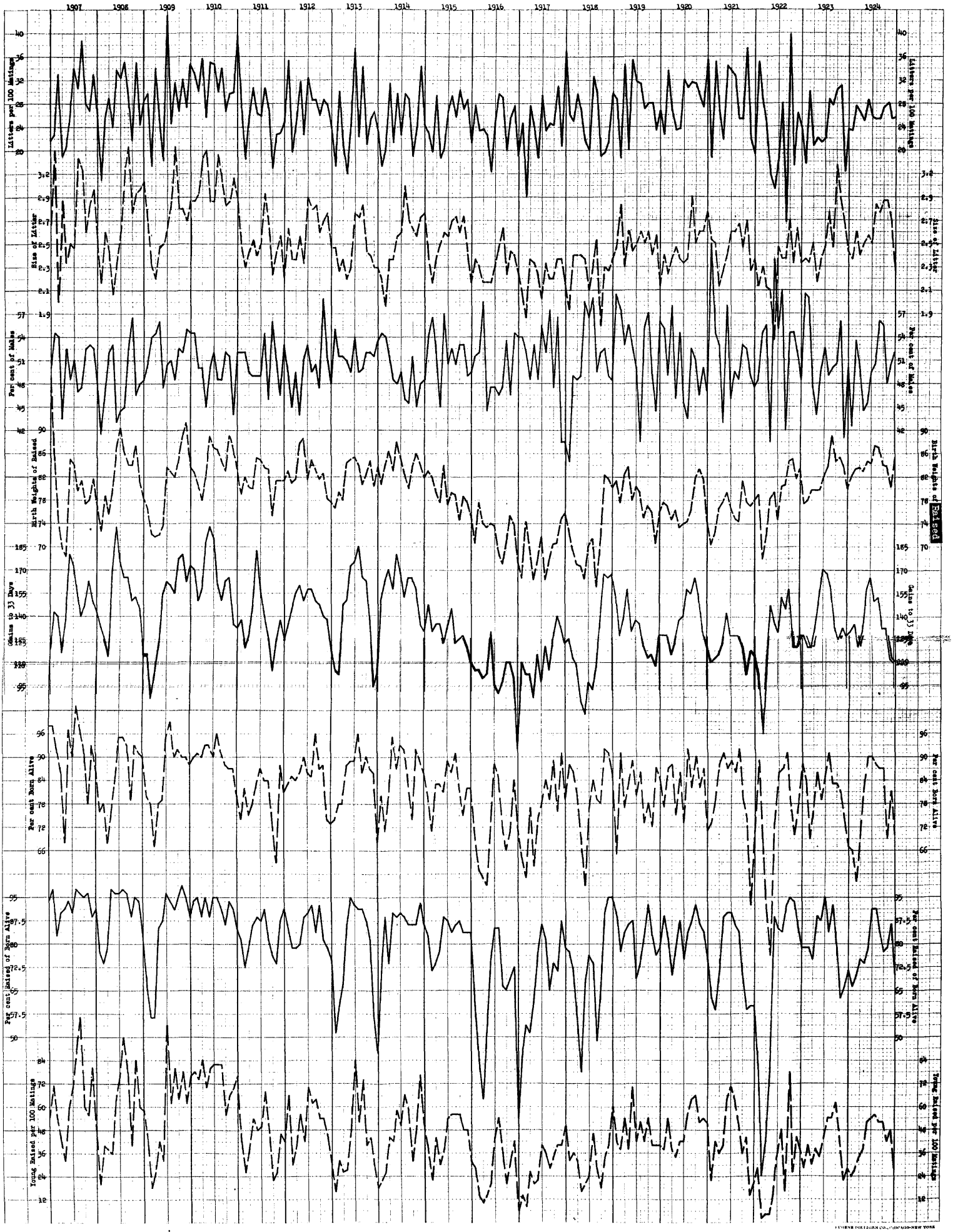
Year	Month	Litters per 100 matings	Average size of litter	Per cent males	Average birth weight of those raised	Average gain to 33 days	Per cent born alive	Per cent raised of born alive	Young raised per 100 matings	Number of young born
					Grams	Grams				
1921	1	18.59	2.53	65.88	70.48	108.87	73.24	62.94	21.87	86
	2	34.86	2.51	54.35	72.31	111.58	78.81	58.24	41.21	138
	3	26.64	2.14	52.94	76.55	115.81	88.03	71.05	36.42	105
	4	21.56	2.25	43.21	77.74	121.54	91.01	88.30	40.72	81
	5	34.48	2.40	57.93	79.40	143.45	86.66	90.39	63.40	149
	6	33.71	2.59	46.05	76.71	127.60	88.94	90.13	70.29	153
	7	32.80	2.61	49.36	74.92	126.35	86.44	86.26	63.44	159
	8	25.25	2.65	48.41	74.48	128.37	91.79	84.28	51.54	127
	9	25.27	2.46	53.10	81.38	119.82	78.99	69.81	35.16	113
	10	37.22	2.71	52.38	77.59	101.93	74.01	58.22	43.59	190
	11	21.74	2.28	48.78	76.96	117.23	51.57	60.27	14.67	91
	12	19.35	2.38	47.50	77.94	116.12	71.44	60.10	20.50	81
1922	1	35.04	2.14	48.48	79.04	102.98	89.03	41.60	28.36	135
	2	28.65	2.30	54.74	68.00	64.33	68.85	4.43	1.86	106
	3	24.35	2.13	55.41	72.00	102.00	49.92	15.92	3.74	83
	4	15.63	2.10	40.54	78.33	146.84	39.27	39.60	4.69	42
	5	13.20	1.67	64.00	79.18	138.35	73.44	88.26	14.95	25
	6	18.87	2.45	55.10	74.62	131.14	85.82	85.44	34.91	49
	7	27.92	2.37	60.00	80.43	151.57	86.73	83.36	47.46	71
	8	7.52	2.38	42.11	80.53	145.76	91.26	93.11	15.97	19
	9	39.81	2.70	54.46	84.57	157.63	78.16	95.23	77.78	116
	10	17.23	2.33	54.35	85.07	118.79	70.33	93.21	25.42	49
	11	26.45	2.63	51.90	81.51	121.06	77.65	85.37	43.80	84
	12	23.84	2.32	48.68	83.40	127.78	87.89	78.57	38.57	79
1923	1	17.72	2.38	59.68	77.43	127.52	84.35	78.58	28.62	62
	2	30.11	2.33	59.00	77.86	120.80	68.64	79.00	39.21	100
	3	20.78	2.49	47.50	79.74	119.52	77.70	75.52	29.09	87
	4	21.89	2.16	43.75	79.73	133.24	85.81	89.19	37.28	80
	5	21.20	2.36	49.44	79.55	151.79	79.12	88.10	34.80	92
	6	21.86	2.48	52.63	82.15	169.58	84.68	95.61	43.17	99
	7	28.65	2.77	48.87	83.72	168.17	91.11	83.77	53.52	147
	8	27.65	2.46	50.00	89.14	158.67	83.16	92.71	54.23	128
	9	30.43	3.16	50.28	84.63	132.26	83.20	79.62	61.41	177
	10	31.14	2.86	56.21	85.49	125.63	80.57	62.08	41.71	160
	11	16.18	2.68	41.10	83.65	133.30	74.29	66.69	21.39	75
	12	23.67	2.42	50.00	79.87	126.32	67.40	71.36	27.35	109

Table 11 Cont.

Monthly Indices

Year	Month	Litters per 100 matings	Average size of litter	Per cent males	Average birth weight of those raised	Average gain to 33 days	Per cent born alive	Per cent raised of born alive	Young raised per 100 matings	Number of young born
					Grams	Grams				
1924	1	23.22	2.36	42.55	81.91	130.90	66.02	66.53	23.78	99
	2	27.83	2.59	53.51	83.34	134.40	57.82	69.48	28.44	119
	3	26.34	2.41	50.00	83.76	119.66	70.25	75.62	33.78	111
	4	25.00	2.50	44.66	83.02	130.86	81.69	73.31	38.10	105
	5	28.63	2.58	45.67	84.52	156.88	89.98	78.60	51.53	129
	6	25.71	2.49	49.55	84.45	166.03	89.86	91.45	53.14	112
	7	25.49	2.82	50.37	87.39	150.17	88.41	90.82	56.18	138
	8	25.33	2.76	55.80	86.87	151.46	87.46	83.87	51.17	138
	9	27.18	2.87	55.70	84.04	132.06	87.39	77.78	51.28	152
	10	27.99	2.85	47.88	83.51	133.60	68.51	78.71	42.22	168
	11	25.49	2.71	50.36	80.22	113.25	80.97	86.19	47.55	141
	12	25.77	2.28	52.17	85.31	109.40	69.76	70.17	28.69	121

CHART XII MONTHLY INDICES



the females which automatically prevents litters being born to these individuals in the next month. The high and low points of the different years show some tendency toward seasonal effects, but there is much irregularity. There appears to be some tendency for the period May to August to be a little more favorable with relatively high points in the fall in many years. It is striking that the real high points in the late fall or early winter appear to be related to years in which no high point was observed in a spring or summer month.

It is evident that this index was not entirely satisfactory as a measure of the frequency at which litters were produced. Frequency of litters being obviously a much delayed evidence of conditions during a period of over 2 months prior to the time of parturition tends to further complicate its expression.

Size of litter.- As in case of frequency of litter, size of litter is mainly determined at conception, 68 days before the litter is born. There are, however, influences acting throughout pregnancy which may tend to reduce litter size. In case of this index there is apparently some cyclic behavior related to the season. The months of January to April are generally low, while in June to November litter size is usually larger. A few years like 1917, 1918, and 1919 show considerable irregularity and do not bear this out well.

Sex Ratio.- The per cent of males shows much seasonal variation but even with the irregular character of the graph there appears to be a slight tendency for the ends of the years to be high with a drop during the spring and summer months. The exceptions to this are so

frequent, as in 1918, that it can not be considered as following the season closely. Many years indicate that these variations are related to the behavior of the other indices. For instance, in 1909 practically all the other indices show a relatively high point in January with a drop to March and a rise to July while the per cent males goes in the opposite way. Again in 1920, 1921 and 1923 a similar relation is striking but other cases do not bear this out.

In a test of the goodness of fit of the sex ratios in the individual months to the monthly average sex ratio observed 50.58 per cent males, X^2 was found to equal 173.65. X^2 tables do not go as high as n = 216 (217 months were used) but Fisher (1925) suggests use of $\sqrt{2x^2} - \sqrt{2n-1}$ in which differences significantly greater than 2 indicate that the data do not conform to expectation. Substituting for these values 18.64 - 20.76 = -2.12 which is in close agreement with expectation. Such is to be expected since most all of the X^2 values for individual months were low, only 3 causing any suspicion of significant departures from expectation, October 1912, July 1919, and January 1921, in which the X^2 values were respectively 6, 4, and 8. It is of course possible that variations in the sex ratio might be associated with the season and still such might not show wider departures from normal expectation than would be expected by chance. There is indication of seasonal variation in that the monthly sex ratios show consecutive departure in the same direction, particularly in the fall and winter.

Birth weights and gains.- The birth weights and gains are both shown for the month in which they were born and both behaved very

similarly in most years. This is probably due to the fact that the gains made in a certain month are evidently affected by the same influences that act on the fetus in utero and affect the birth weights of the individuals born in that month, tho there is some indication that birth weights are a little slower in reacting than gains.

Both birth weights and gains show a rather regular cycle over most of the years, the low points being in the winter and the high points in the late spring or early summer (May and June). The years of unfavorable conditions, 1915, 1916, 1917, and 1918 are particularly prominent in these data. With some zigzaging both show a rapid decline beginning with approximately December 1914. It may also be noted in this connection that in the favorable year, 1910, the customary drop in late winter and early spring was much abbreviated, so that the curves continued with a small break to rise from February 1909 to the highest point in the entire 18 years in May 1910.

Mortality.- As in the case of the weights and gains, the per cent born alive and the per cent raised of born alive are recorded for the months in which the individuals were born, and are closely related, generally showing low points in the winter or early spring and high points in the summer or fall. April was frequently a low month, while July was high for the per cent born alive. As in the gains, the per cent raised is affected by the same conditions which affect the per cent born alive, i. e., while the young are in utero the mortality is increased in the same way as the mortality of individuals between birth and weaning is affected. The fluctuations in the per cent raised are somewhat greater than the fluctuations in the per cent

born alive, probably because the dam acts somewhat as a buffer to changes in environment affecting the young in utero.

Net fertility.- The net fertility is a combination of four of the other characters and therefore should show somewhat the same general course. It is essentially the product of the litters per 100 matings, size of litter, per cent born alive, and per cent raised of born alive, except that the two latter indices were corrected to eliminate the effects of size of litter and sex. The general course of the net fertility curve is low late in the winter and early spring, reaching a peak in midsummer or early fall.

Averages for combined months.- In studying the seasonal relations of the indices, the data for all months of January, all months of February, etc were combined and treated as one year. This was virtually the weighted averages for each of the months. In this way the indices for each of the combined months are based on large numbers of individuals, the smallest numbers in any month being 830 litters and 1,973 individuals in February. The records for the combined months are given in Tables 12 and 13, together with comparisons for the averages calculated using corrected and uncorrected weights and mortality percentages. This was done for the purpose of estimating the effect of the correction factors used on the several groups of data. As is quite evident, eliminating the effect of size of litter and sex on weights and mortality has had little effect on the relative ranking of different months for a particular index, but it has tended to bring out more strikingly the variations.

Table 12

Averages for Fertility Characters in Combined Months from 1906 to 1924 (Litters 1 to 6)

Month	Matings	Litters	Individuals	Litters per 100 matings	Size of litter	Sex ratio	Born alive		Raised of born alive	
							Corrected	Uncorrected	Corrected	Uncorrected
	Number	Number	Number	Number	Number	% ♂s	Per cent	Per cent	Per cent	Per cent
January	3,738	979	2,400	26.19	2.45	52.45	78.28	79.45	73.60	74.03
February	3,692	830	1,973	22.48	2.38	52.19	76.87	78.01	69.22	69.62
March	3,695	1,055	2,563	28.55	2.43	51.79	77.60	78.60	71.02	71.40
April	3,591	844	2,085	23.50	2.47	47.76	80.38	81.11	82.00	82.35
May	3,491	904	2,224	25.90	2.46	50.52	85.21	85.57	87.67	87.85
June	3,541	1,061	2,734	29.96	2.58	50.48	88.12	87.99	90.06	90.03
July	3,540	1,053	2,924	29.75	2.78	49.41	90.08	88.33	88.88	88.20
August	3,632	1,076	3,032	29.63	2.82	49.60	87.00	85.40	85.87	85.27
September	3,651	919	2,405	25.17	2.62	52.47	83.65	83.52	85.53	85.48
October	3,773	1,094	2,916	29.00	2.67	51.32	81.26	80.83	83.07	82.88
November	3,917	1,028	2,715	26.24	2.64	49.03	84.26	84.36	83.83	83.89
December	3,899	1,080	2,729	27.70	2.53	50.39	79.66	80.27	78.80	79.09
Average	44,160[1]	11,923[1]	30,700[1]	27.00	2.57	50.58	83.01	83.01	82.30	82.30

[1]Total not average.

Table 13

Averages for Birth and Weaning Weights and Gains in Combined Months from 1906 to 1924 (Litters of 1 to 6)

Month	Birth weights						Weaning weights		Gains to weaning	
	Born dead		Died		Raised					
	Corrected	Uncorrected	Corrected	Uncorrected	Corrected	Uncorrected	Corrected	Uncorrected	Corrected	Uncorrected
	Grams	Grams	Grams	Grams	Grams	Grams	Grams	Grams	Grams	Grams
January	59.57	59.82	70.02	72.19	78.91	80.67	214.17	217.22	135.26	136.55
February	61.13	64.17	69.58	71.81	78.76	80.99	206.67	210.74	127.91	129.75
March	59.62	61.20	68.28	70.14	78.30	80.23	213.54	217.03	135.24	136.80
April	58.53	60.52	67.36	67.85	79.94	80.76	227.64	228.57	147.70	147.81
May	67.07	69.59	72.38	72.55	83.08	83.85	245.80	247.07	162.72	163.22
June	66.07	66.14	70.52	69.35	82.24	82.13	238.75	238.29	156.51	156.16
July	67.03	62.86	66.99	62.51	81.22	79.61	229.49	226.09	148.27	146.48
August	65.56	64.20	69.14	65.81	80.77	78.46	226.03	221.19	145.26	142.73
September	67.38	65.98	72.73	72.16	81.00	80.74	226.82	226.19	145.82	145.45
October	63.55	62.64	72.97	72.12	83.39	82.46	227.51	225.73	144.12	143.27
November	65.37	64.48	72.08	71.26	81.64	81.43	213.58	213.06	131.94	131.63
December	61.86	61.82	72.08	72.68	80.28	81.42	211.01	213.18	130.73	131.76
Average	63.25	63.32	70.26	70.24	81.01	81.03	224.62	224.42	143.61	143.39

Size of litter tends to offset the influence of other factors on weights and mortality; for instance, if conditions are unfavorable, litters will be small in size, but as a result of this birth weights will be correspondingly larger, etc. Consequently the correction for the elimination of the effect of size of litter has tended to reduce the lower values and raise the higher ones. The elimination of the effect of sex has been relatively unimportant because the sexes were nearly equally distributed in the combined months, but this no doubt had an important effect in individual months where the numbers were smaller and the sex ratios showed more variation. The data for the combined months as presented in Chart XIII afford a better opportunity for studying the average variation of the different indices with the seasons than does Chart XII showing the variation over the entire period.

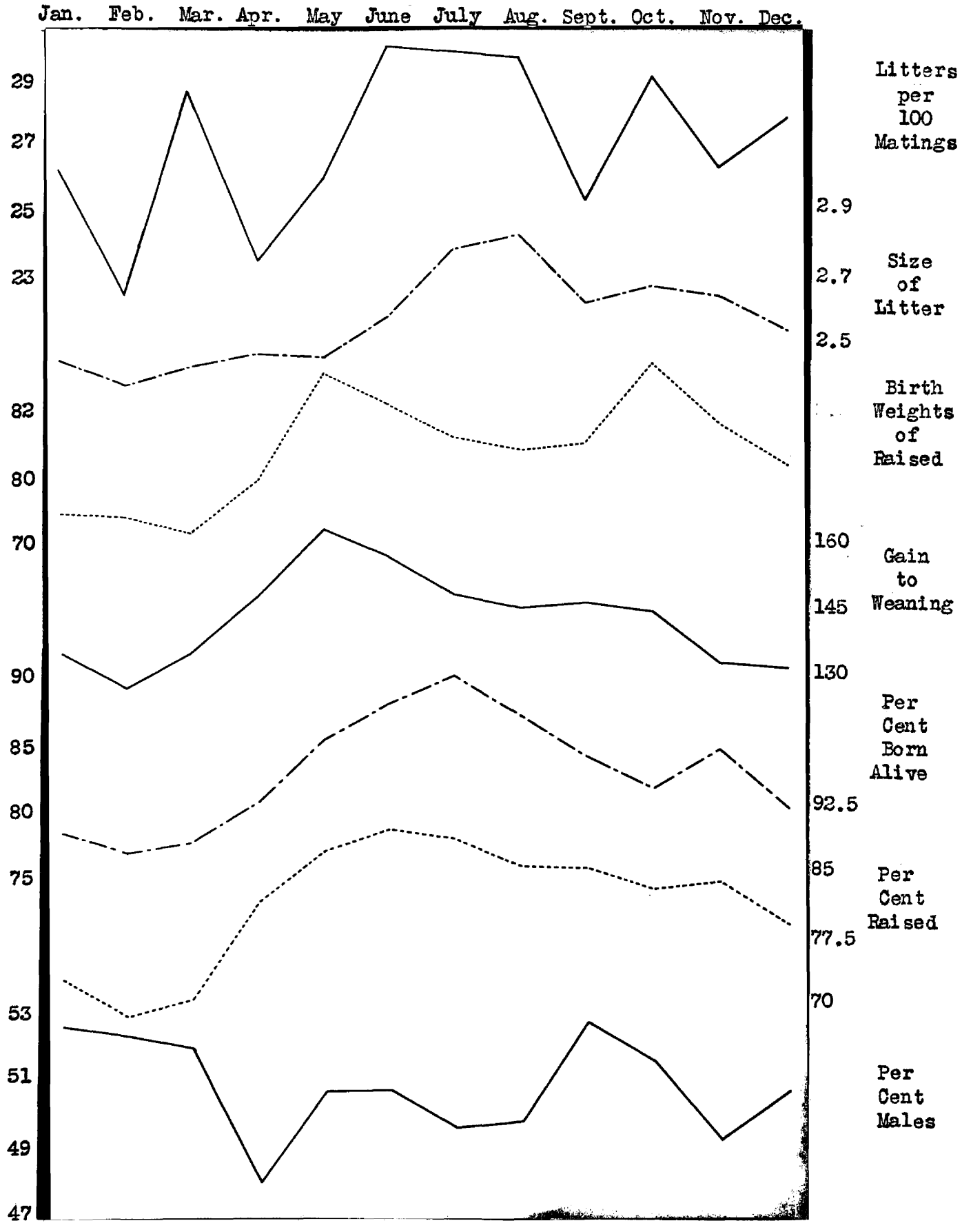
It is indeed interesting that litters per 100 matings in the combined months shows somewhat the same tendency to alternate in successive months, as was observed to a greater extent in the individual months. For the data of the combined months the only case in which the alternating relationship is not shown in successive months is during the summer in June, July, and August, the most favorable season. The beginning of this effect is also shown in May; all other months alternate.

Size of litter for the 6 month period, December to May, is below the average, while the 6 months, June to November, are above the average. The high points for size of litter are in July and August, which appear to be considerably more favorable than other months.

The birth weight curve is distinctly bimodal, showing high points in the spring and the fall. Taken together the two months, May and June,

Chart XIII

Monthly Indices for Combined Months (Litters 1 to 6)



form the highest mode and the second mode which is the highest for any one month is in October. The tendency for several of the indices to rise in the fall was also evident in the curves for the individual months.

The gains showed much the same variation over the year as birth weights, except that the peak in the spring was much more pronounced, and there was but slight evidence of the fall mode. The maximum gains were made by those born during the month of May.

The mortality curves were similar in shape. Both showed low points in December, January, February, and March followed by a rapid rise to the mode in July for those born alive and to a mode in June for those raised. Particularly large percentages of those born in May, June, and July were raised.

The per cent of males, though the differences are small, shows a high point in January followed by a gradual drop to July and August, except for the low point in April. The per cent of males rises to another high point in September, dropping again to a low point in November. There is some indication of a reciprocal relation of this curve to most of the other indices.

Discussion.- Seasonal variation in the breeding of wild animals is common. Under domestication it appears that most classes of livestock breed thruout the year according to the desires of the stockman as to when he wants the young to come, based on likely market demand and when the young can be best and most satisfactorily cared for. Little consideration is given to the relative number of young, the mortality or the birth weights and rate of growth of young born in the different seasons of the year.

Probably more attention has been given to the number of young produced at birth in sheep than in any of the other domestic animals. The practice of flushing ewes to increase the lamb crop is a common practice in some sections and by certain stockmen, but the merit of this practice and the time when the extra feeding should be done has not been established without some question of doubt. Nichols (1924) summarized work on fertility in sheep and concluded that flushing increased fertility thru the production of a larger percentage of multiple births. Marshall & Potts (1924) arrived at a similar conclusion from their experiments. Castle (1924) also found in the study of another flock that twinning was more a product of vigor and environmental conditions than it was hereditary.

From a study of herd book records of Angus and Hereford cattle Cole and Rodolfo (1925) found the largest percentage of twins in August with a greater tendency to twinning in the late summer and early fall than in other seasons. Numerous observations on seasonal variations in the fertility of rodents and other laboratory animals have been reported. Of interest in this connection are the findings of Feldman (1925) in which the maximum litter sizes in the rat were found to occur in June, followed by a steady decline to October, and another increase in November and December; King (1927) reported that the numbers of litters and size of litters in mice, dogs and swine were greater during the first 6 months than during the second 6 months of the year, but fertility in the rat was fairly constant over the entire year; Hanson and Heys (1927) found that season of birth influenced the 40 day weight of rats; Parkes (1924 and 1926 - IX) found the minimum litter size in March and the maximum in July; Moyer (1924) pointed out that the birth rate in guinea pigs was lowered from November to March due to reduced vigor and Wright (1922) pointed out that all measured factors having a bearing on vigor were influenced by the season.

Riddle (1924) found that the rate of ovulation in pigeons followed changes in the temperature thruout the year. More fundamental relations were also established. The blood sugar which is closely related to ovulation was reduced by insulin, confinement, and cold weather. The size of the thyroid and suprarenal glands and the blood calcium which is associated with the former have also been found to vary (1926). The various organs of the rabbit undergo rhythmic changes in weight which are associated with the season (Brown et al/1924). Tho the relation of these changes to reproduction is not so clearly established as in the pigeon it may be assumed that some or more probably the interrelation between several have a bearing on the physiological tonus of the animal and so influence its reproductive capacity.

From the data presented in the present study for the combined months the summer months, June, July and August, appear to be on the average the most favorable for frequency of litter, size of litter and per cent born alive in the guinea pig. The per cent raised of those born alive is also high in these months but the high period begins for those born in May. Definite peaks in the birth weight and gain curves point toward those born in May as the optimum; such gains being made during the month of June. Most of the indices are generally high during the summer and extending into the early fall, birth weights showing a second mode for those born in October.

The winter months of December, January, February and March were on the average generally the most unfavorable for the expression of the indices, a single high point in the frequency of litters in March being the exception.

With the expression of the various indices being highest during the summer the favorable conditions in the environment causing such expression particularly in frequency and size of litter must have occurred in the spring, and probably in the early spring, assuming that the reaction in the way of fertile matings is almost immediate while the number of ova produced which is the main effect on size of litter requires somewhat longer to be effected. The expression of birth weights is somewhat earlier but gives ample time for the dam to be influenced and still transfer the effect to the young in utero during the last half of the gestation period, this being the time when the major part of the growth of the foetus occurs and the time when variations in the birth weights would most likely result. Gains appear to be more closely associated with the birth weights of the individuals than to temporary environment as shown by the parallelism of these 2 curves. Per cent raised either comes closest to being an expression of conditions after birth as it is amongst the first to show a sharp rise and is measured over a period of 33 days after birth, or per cent raised is effected by conditions quite different from those influencing the other indices.

In considering the monthly variations one should not overlook the fact that the basic data for the calculations is taken from the records of several different families which no doubt react differently to a specific influence. Further the data for the combined months cannot be thought of as representative for any particular year but may be taken as an average expression of conditions in the seasons for the 18 year period. Variations in temperature, sunshine, rainfall, or other meteorological conditions within and without the heated colony house cause ex-

treme variations from the normal but it is felt that fairly accurate factors for eliminating the effect of season may be obtained from the combined data for general purposes or for these records for particular months of particular years by multiplying by the product of the reciprocal of the value in the combined month in question by the average for the 12 combined months for that index.

The discussion of the seasonal variations in the indices would not be complete without reference to the sex ratio. The variations in the individual months are so irregular that they are related to the other indices with some difficulty but in the combined months the percentage of males is high for January, February and March when other indices are low and high in September and October when the indices for mortality and gains are dropping. This would point toward a higher prenatal mortality of females when conditions are poor. This is not in conformity with the general belief of greater prenatal mortality of males. Parkes (1926 VIII) found the sex ratios in swine to be relatively constant over the season. McPhee (1927) however pointed out the need for caution in the use of herd book data in the study of sex ratios and litter size in swine. Seasonal variations in the sex ratio in dogs was reported by Szuman (1925) the proportion of males being highest in February and low in August and September. Christie (1925) also called attention to seasonal variations in the sex ratio of pigeons. King and Stotzenberg (1915) found in the rat that litters cast in the spring had a lower per cent of males while those born in the summer months had a high per cent of males; Parkes (1926 IX) found in mice the highest per cent of males in litters born in October to December, 55.9% and the lowest for those

born in April to June 48.2% males; while Sumner, McDaniel, and Hustis (1922) found a biennial rhythm in sex ratios in peromyscus, males predominating in the periods February to April and August to October, while females predominated in litters born during the rest of the year. Seasonal and annual fluctuations in the sex ratio of man have been commented upon by various authors. It is of interest that Dusing (cited by Parkes 1926) reported seasonal variations in the sex ratio of Prussians which were associated with the conception rate, a high proportion of males being associated with a low conception rate. Many attempts to modify sex ratios have been reported with a considerable lack of uniformity in the results; alcohol treatments were found by Pearl (1917) Bluhm (1921) Danforth (1926), and Chaudhuri (1928) to increase the percentage of males, while Crew (1926) and MacDowell (1928) found no effect from treatment by inhalation or injection of either parent. Reference has been made to a few of the varied opinions on this question to bring out the uncertainty of seasonal variations in sex ratios. With the large amount of data on which this study is based and the fact that many of the differences, particularly the larger ones, are more than three times the probable error, it seems proper to conclude that there were significant seasonal variations in the sex ratio in the guinea pig data studied.

Correlations of Monthly Indices.

The primary object of determining the monthly indices was for calculating the relation between the various measurable components of fertility and related factors over several months. The monthly indices were first coded according to Table 14 and simple correlations were cal-

Table 14

Coding of Monthly Indices

Class	Litters per 100 matings	Average size of litter	Per cent males	Average birth weight of those raised	Average gain to 33 days	Per cent born alive	Per cent raised of born alive	Young raised per 100 matings
0	15.49	1.83	40.49	65.99	90.99	63.99	44.99	10.00
1	15.50-18.49	1.84-2.00	40.50-42.99	66.00-68.99	91.00-101.99	64.00-67.99	45.00-50.99	10.01-20.00
2	18.50-21.49	2.01-2.17	43.00-45.49	69.00-71.99	102.00-112.99	68.00-71.99	51.00-56.99	20.01-30.00
3	21.50-24.49	2.18-2.34	45.50-47.99	72.00-74.99	113.00-123.99	72.00-75.99	57.00-62.99	30.01-40.00
4	24.50-27.49	2.35-2.51	48.00-50.49	75.00-77.99	124.00-134.99	76.00-79.99	63.00-68.99	40.01-50.00
5	27.50-30.49	2.52-2.68	50.50-52.99	78.00-80.99	135.00-145.99	80.00-83.99	69.00-74.99	50.01-60.00
6	30.50-33.49	2.69-2.85	53.00-55.49	81.00-83.99	146.00-156.99	84.00-87.99	75.00-80.99	60.01-70.00
7	33.50-36.49	2.86-3.02	55.50-57.99	84.00-86.99	157.00-167.99	88.00-91.99	81.00-86.99	70.01-80.00
8	36.50-39.49	3.03-3.19	58.00-60.49	87.00-89.99	168.00-178.99	92.00-95.99	87.00-92.99	80.01-90.00
9	39.50	3.20	60.50	90.00	179.00	96.00	93.00	90.01

culated between the eight monthly indices within the same month and for each one with each of the others for the four preceding and four succeeding months, using as a basis the monthly indices from December 1906 to December 1924. The correlations thus indicated the relationship between the different indices over a 9-months period. The correlation coefficients calculated in this way are presented in Tables 15 to 22 and in Charts XIV to XIX. The month designated as 0 refers to the basic month for the group. For example, the correlations of litters per 100 matings with the other indices are given for litters per 100 matings born in the 0 month as related to itself, size of litter, etc. in each of the other months. Those at the left of the 0 month and designated by minus signs refer to months preceding and those at the right and designated by plus signs refer to months succeeding the 0 month.

As was previously explained, the indices for gains and per cent raised of born alive were recorded for the month in which they were born but were really expressed 33 days later. For this reason in plotting the correlation coefficients they have been advanced 33 days in their relation to the other indices and vice versa. In the Tables they have been advanced one month. Net fertility was calculated for the guinea pigs born in a certain month and therefore applies to a combination of conditions before birth and 33 days after birth. It therefore is not comparable to the expressions at birth nor is it comparable with expressions of conditions during the succeeding month. Its relation to the other indices is presented, however, as it is the net measure of fertility, being the number of young raised from those born in a particular month per 100 matings in that month. Any other means of calculating an index of this sort appeared to be subject to similar or greater criticism.

In presenting the correlation coefficients the probable errors are not given, but they are easily estimated. The correlations are based on 213 months' records in all cases, the first 4 months' indices which were calculated from smaller numbers of individuals only being used in the correlations with indices in months preceding and succeeding the 0 month. The formula for the probable error for the correlation coefficient is $0.6745 \frac{1 - r^2}{\sqrt{n}}$ where r is the correlation coefficient and n is the number of pairs correlated. The probable error of any coefficient may thus be determined by multiplying $1 - r^2$ by .046. The probable error is .046 for correlations from .00 to .10 and is reduced for larger coefficients.

It will be noted that in general the 9 correlations between the index of a particular character and those for 9 successive indices of another character form curves starting with lower values and gradually rising to higher values, dropping off toward the end to lower values. For the purpose of final analysis it is desired to know the point at which the maximum relation between different indices occurs which makes necessary an estimation of the mode of each curve of the correlation coefficients. A thoroughly satisfactory method of estimating the true course of the curves was not evident. One method was to fit some mathematical formula to each, but the question arose as to which points at the ends of each curve to omit and what equation to use which would obviously be different for each curve. The choice of such a method is purely arbitrary, and the measure of success is the judgment of the eye. It therefore seemed as well to attempt to fit them by the eye in the first place when so much irregularity existed. Charts XIV to XIX show the relationship of each index to every other index over the 9 months period but the course of the smoothed curves is not given since it was felt such would be more confusing than clarifying and might be misleading. The point at which the mode appeared to be located is indicated by an

arrow. The mid point of the months designated as in Tables 15 to 22 are designated at the bottom of the charts. The indices to which each curve applies are indicated. The distance between the parallel horizontal lines represents values from 0 to 1.00 on the correlation scale.

The fact that certain of the indices are expressions of happenings several months before makes their discussion rather confusing. Further than this the relations are very complicated, and it is extremely difficult to disentangle them. The correlations are discussed below, first with reference to their relative magnitude and finally with reference to the relationship and time interval between expressions of maximum relationships, from which estimates of the major influences of common conditions on the different characters have been made. The interpretation of the correlations must be made on the basis of related reaction to simultaneous or related conditions and not on a cause and effect basis, since in general such would not have any basis in reason.

Litters per 100 matings.- The negative relation between litters per 100 matings produced in 1 month and those produced in a preceding or succeeding month referred to as causing the sawtooth character of the graph of the monthly indices is also brought out in the correlations of frequency of litter with itself in different months. It is rather striking that there should be no relation between successive months ($r = -.04$) which of course is not significant. The correlations 2 and 3 months distant, .12 and .13, respectively, are positive and approach significance. This simply bears out the assumption of the influence of frequency of litter in one month on frequency of litters in successive months, i. e. when conditions are favorable the majority of the available females produce litters, thus preventing them from brood-

Table 15

Coefficients of correlation between litters per 100 matings in the zero month and the various monthly indices over a 9-months period

	Preceding and succeeding months									
	-4	-3	-2	-1	0	+1	+2	+3	+4	+5
Litters per 100 matings	+.029	+.133	+.120	-.042	+1.000	-.042	+.120	+.133	.029	
Size of litter	+.060	+.152	+.087	+.207	+.460	+.301	+.259	+.114	+.142	
Birth weights of raised	-.003	+.009	+.165	+.220	+.204	+.059	+.070	+.137	+.015	
Gain to weaning		+.008	+.205	+.369	+.274	+.206	+.123	+.050	+.061	-.070
Per cent born alive	+.070	+.135	+.156	+.397	+.298	+.198	+.051	+.065	-.014	
Per cent raised of born alive		+.101	+.128	+.345	+.384	+.195	+.133	+.074	-.002	-.045
Net fertility	+.117	+.179	+.259	+.268	+.718	+.173	+.192	+.166	+.034	
Per cent males	+.107	-.196	-.017	-.130	-.048	-.128	-.032	-.008	+.054	

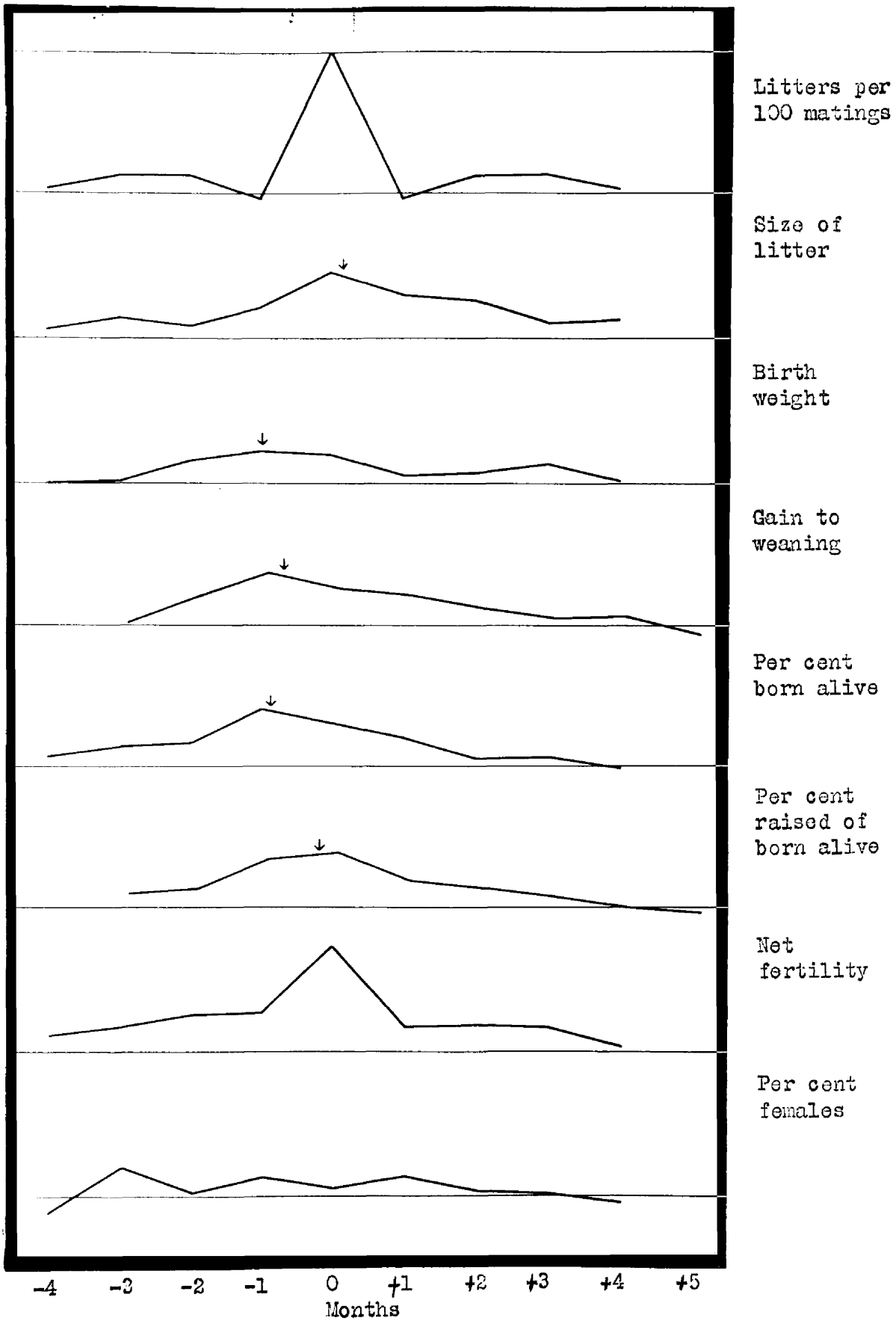
ing in the next month. This relationship is shown in various of the correlation curves and evidently is an important factor in their interpretation. The general run of the correlations of frequency of litter with the other indices are lower than for the other groups of correlations.

Size of litter is the most closely related index to frequency of litter. The highest correlation is .46 within the same month. There are more of the monthly relationships with size of litter above the point of significance than for any other index, six of the months, namely, 0, +1, +2, -1, -3, and +4 being above .14. There is an indication of a slight delay in the expression of size of litter as compared with frequency.

It is quite obvious that these two indices are largely determined at the time of conception, but the influences must also be operative before conception, and both may be modified during gestation, frequency of litter by abortions and complete resorption of litters, and size of litter by resorption of individuals. The same environmental effects may, however, not operate at the same time on both indices and the two may respond differently. There is some indication of differences in response as the curve of the correlation coefficients between the two is maintained higher for following (+) months than for preceding (-) months. This departure from symmetry appears to be about one month or more. This thus indicates that size of litter, while evidencing the maximum effect of a particular influence in the same month, as frequency of litter, is somewhat slower in its reaction showing more lag in its general response. The lag of the maximum correlation between frequency of litter and litter size was estimated from the mode of the correlation curve at +5 days. Assuming that the latest that frequency of litter

Chart XIV

Correlations between Litters per 100 Matings and other Indices.



could be influenced, would be at conception, size of litter being 5 days slower in responding, would be affected in litters conceived 5 days later. Thus conditions associated with frequency at conception are associated with the number of ova produced by females conceiving 5 days later.

Next to size of litter, per cent born alive is most closely related to frequency of litter. The maximum correlation was .40 with the per cent born alive in the -1 month. There were four other months showing possible significant relations, i. e., 0, +1, -2, and -3, in the order given. As one would expect, per cent born alive reacts somewhat more promptly to a common influence than frequency of litter. It is readily understood how an extremely unfavorable environmental condition even acting at birth, such as extreme cold, might destroy entire litters. However, as indicated by the correlation coefficients, the reaction to such immediate conditions is not of primary importance or the time relations would have to be more widely separated than one month. Three of the five significant correlations are with per cent born alive in months before the 0 month with the estimated mode of the maximum relation 26 days before the time of expression of frequency of litter. Calculating back the young expressing the maximum influence of per cent born alive were at the 26th day of the gestation period[1] when the litters by which frequency was measured were conceived. Thus it may be assumed that the maximum concomitant influence on frequency of litter and per cent born alive occur, respectively, at conception and at the 26th day of gestation. The course of the curve showing more lag in the 0 and + months than in - months indicates that the influence on

[1] The gestation period varies from 65 to 71 days but for convenience it has been here considered as 68 days.

per cent born alive is greater prior to the 26th day of gestation than after that point is reached.

The correlation of frequency of litter with per cent raised of born alive was .38 in the 0 month, .34 in the -1 and .19 in the +1 months. The mode of this curve was estimated at -5 days. The per cent raised is expressed 33 days after birth, therefore those showing the maximum relation for per cent raised with frequency of litter are born 38 days before the latter. Therefore, at the time those expressing frequency of litter are conceived, -68 days, those expressing per cent raised are at the 38th day of the gestation period.

The maximum relations with gain and birth weights were .37 and .22 respectively for the -1 month. Gains showed significant correlations in four months, i. e., -1, 0, +1, and -2. Birth weight also showed four significant correlations in the -1, 0, -2, and +3/ months, but the last was only .14, and as it stood out by itself can not be given much consideration. In fact, all of the correlations of frequency of litter with birth weights were relatively low. It is, however, apparent that the mode for the relation of frequency of litter to the weights and gains occurs somewhere during the -1 month and the points were estimated for gains at -20 days and for birth weights at -29 days. The young which showed the effect on gain 20 days before the effect on frequency was apparent were 33 days old at that time. The influence must have operated 68 days before the litters expressing frequency were born. It therefore acted on gain 68 - (20 + 33)=15 days before birth or at the 53rd day of gestation. Similarly from the concomitant variations in frequency of litter and

birth weights the influence on birth weights occurred at the 29th day of gestation, tho the mode of this low flat topped curve was particularly hard to decide upon. The asymmetry of the birth weights and gain correlation curves with frequency of litter indicated that these characteristics were influenced to a greater extent at ages more advanced than the 29th and 53rd days of gestation than before since the larger area of the curves was in the following (+) months.

To summarize it has been pointed out that the correlations between litters per 100 matings and the other indices were not entirely satisfactory because of the irregular behavior of this index from month to month which resulted in generally low correlations, the highest being with size of litter, followed closely by the mortality percentages. The estimated modes of the correlation curves with frequency of litter indicate that the maximum result from a common influence on frequency of litter may be expected to appear 5 days later in size of litter and 29 days earlier in birth weight, 20 days earlier in gain, 26 days earlier in per cent born alive and 5 days earlier in per cent raised, than the time at which the litters are born from which frequency is measured. Assuming that the influence on frequency of litter operates at or before conception the same influence will have its greatest effect on size of litter for those conceived 5 days later and on the other characteristics for litters at or before the following stages of gestation: per cent born alive 26th day, birth weights 29th day, per cent raised 38th day and gain 53rd day of the gestation period.

Size of litter.- Size of litter unlike frequency of litter shows a relatively high correlation with itself in successive months as

Table 16

Coefficients of correlation between size of litter in the zero month and the various monthly indices over a 9-months period

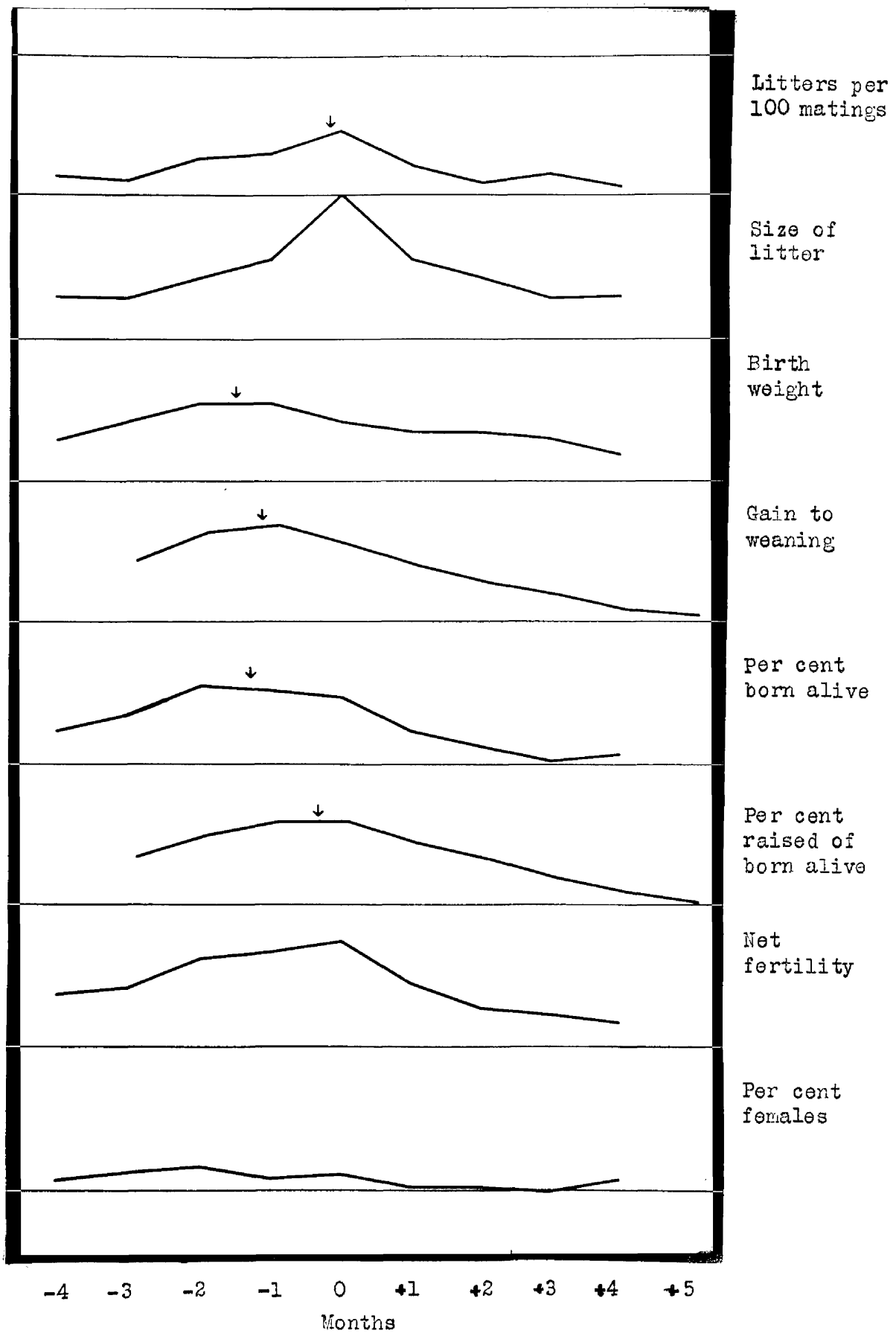
	Preceding and succeeding months									
	-4	-3	-2	-1	0	+1	+2	+3	+4	+5
Litters per 100 matings	+.142	+.114	+.259	+.301	+.460	+.207	+.087	+.152	+.060	
Size of litter	+.301	+.293	+.429	+.563	+1.000	+.563	+.429	+.293	+.301	
Birth weights of raised	+.290	+.429	+.547	+.552	+.417	+.352	+.347	+.296	+.189	
Gain to weaning		+.443	+.628	+.690	+.554	+.397	+.278	+.197	+.075	+.036
Per cent born alive	+.241	+.345	+.543	+.512	+.470	+.241	+.129	+.024	+.068	
Per cent raised of born alive		+.345	+.488	+.591	+.594	+.428	+.315	+.185	+.095	+.014
Net fertility	+.355	+.415	+.611	+.658	+.743	+.440	+.271	+.217	+.155	
Per cent males	-.073	-.124	-.159	-.082	-.113	-.020	-.019	+.009	-.069	

shown in Table 16 and Chart XV. It not only maintains a high correlation between the first and second succeeding months .56 and .46 but for 3 and 4 months away the correlation is practically .30. This tends to indicate that size of litter is the result of an accumulation of environmental effects or that the environmental factors effecting size of litter are associated over the seasons of the year. The values and time relations between size of litter and frequency of litter which are the smallest of the correlations with size of litter were discussed under frequency of litter. The estimated 5 day interval between the expression of size of litter is taken as a basis for the estimate of the time when environmental factors have their maximum effect on the other characteristics. It should be recognized that this time is not so definitely placed and further that the specific point is not necessarily correct for all factors but for convenience this has been adopted so that the explanation may be made more clearly.

The correlations of size of litter with the other indices were relatively high over several months but because of the delayed evidence of the size of litter-at the end of the 68 day gestation period-most of the higher correlations were in the 0 or - months. The highest correlations were .69 and .63 with gain in the -1 and -2 months. For gain in the 0 and -3 months the correlations were .55 and .44 respectively. The correlations of size of litter with gains in the + months were considerably lower but the fact that there was a correlation of .40 between the size of litter and the gains made by the same individuals, after eliminating the effect of litter size

Chart XV

Correlations between Size of Litter and other Indices



should not be lost sight of. The calculation of the correlations between size of litter and the gains made 3 months prior to the measurement of litter size was obviously not sufficient to take account of the length of time over which significant relations occurred.

Smoothing the curve of the time relations between size of litter and gain indicated that the mode was at -34 days. As gain is expressed 33 days after birth, the litters showing the maximum gain were born one day after the litters expressing size of litter were conceived (34 + 33 = 67 days). If size of litter requires 5 days to respond to a definite influence before conception occurs, as was found above in its relation to frequency, this would place the time at which the maximum influence on gains which is associated with size of litter at 6 days before birth or at the 62nd day of gestation.

After gain, percent raised showed the next highest correlations with size of litter .59 for each of the 0 and -1 months. The 3 preceding and two of the succeeding months showed correlations above .30. Here again significant correlations evidently extended for more than 3 preceding months.

Smoothing the curves for the values of r between size of litter in the 0 month and the per cent raised in the preceding and succeeding months indicated that the mode was at -10 days. With the modal relation between size of litter and per cent raised at -10 days the litters for which the per cent raised was measured were born 33 + 10 = 43 days before those for which size of litter was determined. As the major influence on size of litter must have occurred at or before

conception, and which for convenience of explanation is taken as 5 days, the influence of the same factors on per cent raised was operating at least (68 + 5) - (33 + 10) = 30 days before birth or earlier, which would be at or before the 38th day of the gestation period.

There were also relatively high correlations between size of litter and per cent born alive. In the -2 and -1 months the values of r were .54 and .51 respectively and in the 0 month .47. The more important relations were all in the 0 and preceding months but the actual course of this curve in smoothing raised some question. From the observed points it appeared that the mode should lie somewhere between -33 and -45 days with -39 as perhaps the most likely position. As both size of litter and per cent born alive are expressed at birth calculating back 39 days the litters expressing per cent born alive were at the 39th day of the gestation period when the litters expressing size of litter were conceived. Thus the common influence on size of litter and per cent born alive must have been operating on per cent born alive at least as early as the 34th day of the gestation period if we allow 5 days before conception for the influence to operate on litter size.

All of the higher correlations of birth weights with size of litter are in the preceding months tho there is a considerable lag on into the following months, the correlation being .30 in the +3 month. The values of r in the -1 and -2 months are .55 in both cases.

There seemed to be little question of the mode of this curve at -45 days, but there was also some indication of a mode or at least an important lag about 3 to 4 months later which is probably related to the bimodal expression of the birth weights in the seasonal curves. In Chart

XIII it was shown that the favorable season for birth weights based on the expression in several successive months is in the spring which is followed in 2 to 3 months by the most favorable size of litters. Then again about 2 to 3 months later favorable birth weights are attained in the fall (October). This condition in the r values results in a very long period over which significant coefficients were observed between size of litter and birth weights.

Placing the maximum relation between size of litter and birth weights at -45 days and allowing 5 days before conception for the influence to act on size of litter indicates that the common influence on birth weights is operating at or before the 40th day of the gestation period. The correlations of size of litter were relatively high with all the other indices and relatively smooth curves were formed by plotting the correlation coefficients which, except for per cent raised and gains, tapered off quite rapidly 2 or 3 months before or after the month in which size of litter was measured. Most all of the size of litter curves showed quite definite modes tho significant correlations were calculated for several months with each index.

The maximum relations between size of litter and the other indices was evidenced the following number of days prior to the birth of the litters from which size of litter was measured: Frequency 5 days, birth weight 45, gain 34, per cent born alive 39, and per cent raised 10 days. Assuming that it requires 5 days before conception for an influence to act on size of litter, the common influences on size of litter and the other indices were found to have their maximum effect on frequency of

Table 17

Coefficients of correlation between birth weights of raised in the zero month and the various monthly indices over a 9-months period

	Preceding and succeeding months									
	-4	-3	-2	-1	0	+1	+2	+3	+4	+5
Litters per 100 matings	+.015	+.137	+.070	+.059	+.204	+.220	+.165	+.009	-.003	
Size of litter	+.189	+.296	+.347	+.352	+.417	+.552	+.547	+.429	+.290	
Birth weights of raised	+.468	+.534	+.606	+.753	+1.000	+.753	+.606	+.534	+.468	
Gain to weaning		+.460	+.504	+.605	+.747	+.701	+.510	+.381	+.305	+.217
Per cent born alive	+.218	+.302	+.285	+.323	+.435	+.417	+.213	+.101	+.057	
Per cent raised of born alive		+.319	+.319	+.409	+.500	+.538	+.462	+.306	+.176	+.153
Net fertility	+.246	+.326	+.314	+.388	+.518	+.509	+.401	+.217	+.146	
Per cent males	+.008	-.063	-.083	-.094	-.119	-.118	-.016	-.009	+.023	

Table 18

Coefficients of correlation between gains to weaning in the zero month and the various monthly indices over a 9-months period

	Preceding and succeeding months									
	-5	-4	-3	-2	-1	0	+1	+2	+3	+4
Litters per 100 matings	-.070	+.061	+.050	+.123	+.206	+.274	+.369	+.205	+.008	
Size of litter	+.036	+.075	+.197	+.278	+.397	+.554	+.690	+.628	+.443	
Birth weights of raised	+.217	+.305	+.381	+.510	+.701	+.747	+.605	+.504	+.460	
Gain to weaning		+.254	+.364	+.524	+.757	+1.000	+.757	+.524	+.364	+.254
Per cent born alive	+.113	+.223	+.344	+.412	+.551	+.618	+.504	+.279	+.131	
Per cent raised of born alive		+.153	+.223	+.361	+.537	+.694	+.695	+.515	+.332	+.209
Net fertility	+.061	+.189	+.276	+.439	+.601	+.684	+.669	+.470	+.235	
Per cent males	+.101	-.003	-.012	-.103	-.162	-.121	-.108	-.064	+.017	

litter at conception, and on the other indices at the following stages of gestation: per cent born alive 34th, birth weights 40th, per cent raised 38th, and gain 62nd day of the gestation period.

Weights.- Birth weights correlated with birth weights and gains correlated with gains over the 9-months period present similar curves except that the relationship between birth weights evidently extends over a longer time, the correlation for birth weights separated over a period of 4 months being .47, while gains over a similar period show a correlation of .25. The respective coefficients in the third month are .53 and .36; in the second .61 and .52; but in the succeeding months they are very similar, .75 and .76. When considered in reference to each other the maximum relation is between gains made 14 days later than the birth weights were recorded. The correlations between birth weight and gain are relatively very high. With birth weights as a base they are .75 and .70 in the 0 and +1 months. High correlations are maintained in the minus months, being .46 in the -3 month, showing that there is a higher degree of relationship between birth weights and the gains made two or three months before than between birth weights and gains made two or three months later. This shows a relatively high degree of relationship between birth weights which might be designated as intrauterine gain and the gain between birth and weaning, designated as extrauterine growth. This is particularly interesting in that the correlation between the birth weights and the gains made by the same individuals .70 is not quite as large as the correlation between the birth weights and gains made at the same time .75 by different individuals. The 14 days' difference in the expression of maximum relation of gain to birth weights places the time of birth of the 2 groups 19 days apart, those measuring gain being

Chart XVI

Correlations between Birth Weights and other Indices.

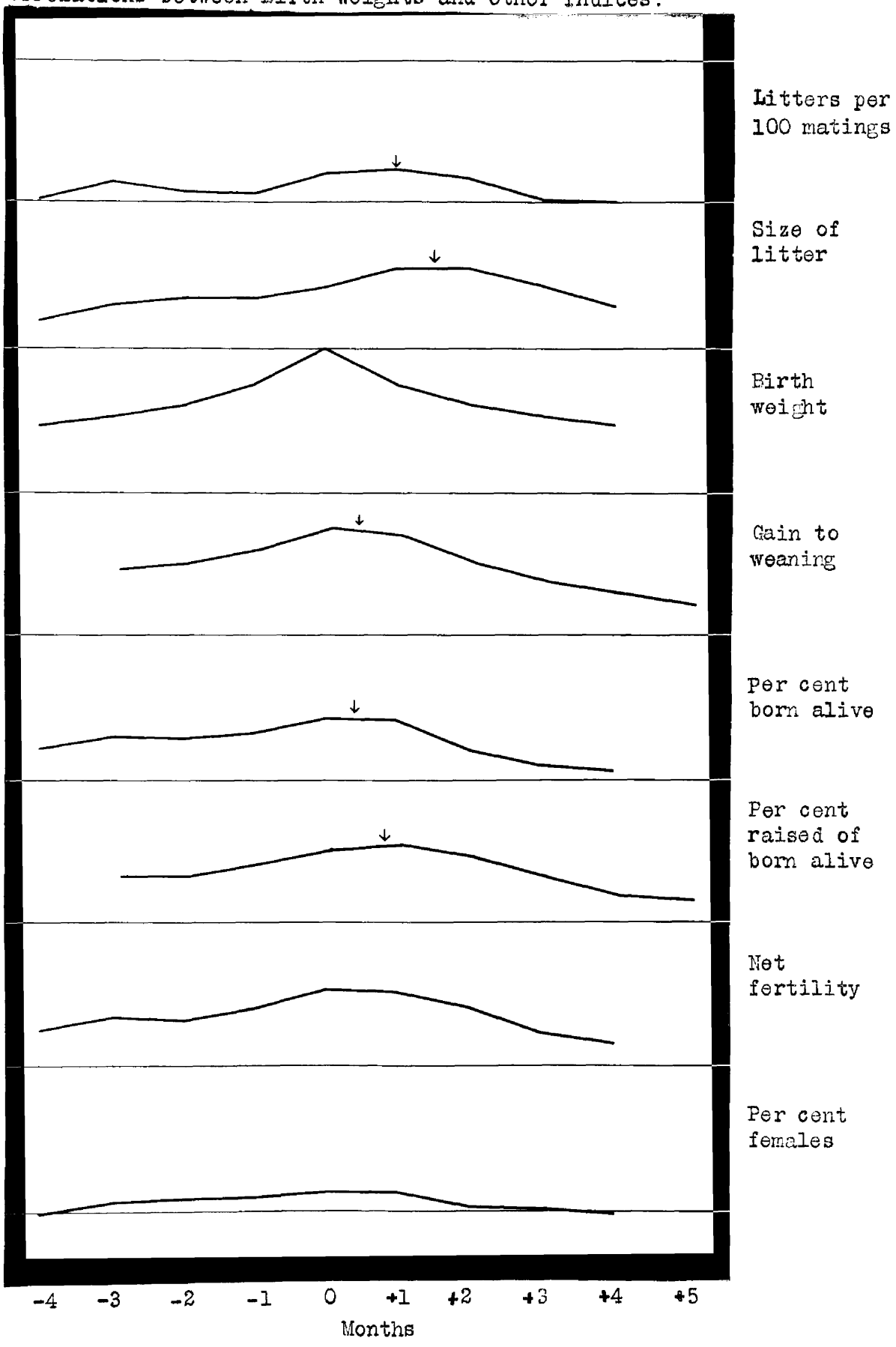
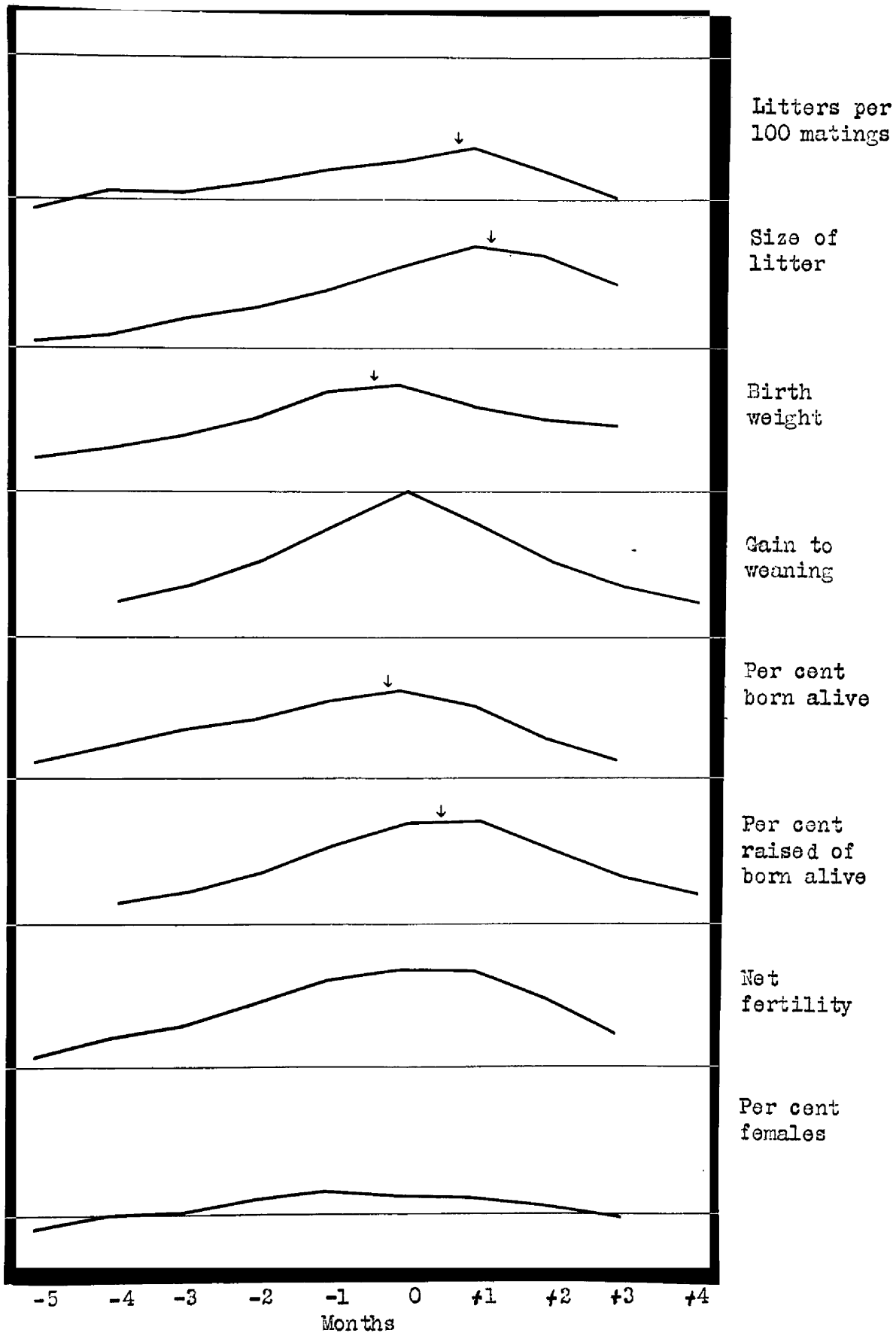


Chart XVII

Correlations between Gains and Other Indices.



born first. It is impossible to set a definite point before which influences acting on birth weights must have operated without basing it on the relation between size and frequency of litter which may not be the same as with the other indices. The time when these indices are influenced will, therefore, be taken up later.

Next to gain the highest correlations with birth weights were with size of litter which have already been discussed under the latter heading. There was found to be 45 days difference between the maximum relations of the two characteristics.

Next to size of litter birth weights were most closely related to per cent raised of born alive. In the +1 month which gives the relation in the same individuals and may possibly have some cause effect basis, the correlation coefficient was .54 and in the 0 month .50. The values of r in the -1, -2, -3, +2, +3, +4, and +5 months were respectively .41, .32, .32, .46, .31, .18, and .15. Thus significant correlations were maintained over a considerable period, tho none were as high as those observed between birth weights and gains. Birth weights and per cent raised are obviously expressed at different times, the former at birth and the latter during the 33-day period following birth. The estimated interval between maximum expressions was 25 days. Tho the mode of this curve is obviously in the +1 month, it is relatively high in the minus months to the extent that it is almost bimodal.

The per cent born alive is less closely related to birth weights than all other indices except frequency of litters. The largest relations between birth weights and per cent born alive were in the 0 and +1 months with correlations of .43 and .42. The values of r in the -1 and -3 months were .32 and .30 respectively, and in the -2, -4, and +2 months .29, .22, and .21. The mode of this

curve was estimated at +12 days but a second mode was also apparent at -90 days, and the curve was relatively high for the entire 4 months preceding 0. With 12 days difference in the expression of the birth weights and per cent born alive resulting from a common influence per cent born alive is affected 12 days earlier in the gestation period than birth weights.

The time relations and correlations of birth weight to frequency of litter have been discussed under the latter heading and it is sufficient to call attention to the fact that the correlations when considered in connection with the other birth weight correlations, were very low none being higher than .22.

A number of the birth weight correlation curves showed a definite bimodal characteristic as previously mentioned for birth weights with frequency of litter, size of litter and per cent born alive and possible indication of a similar nature for per cent raised and gains. The explanation of this characteristic of the birth weight curves appears to lie in the bimodal characteristic of the birth weight index when plotted for the combined months.

The relationships of gain to the other indices are similar to those for birth weights, except that gains in successive months are not so closely correlated as birth weights in successive months. The tendency for the correlations of gains in successive months to be lower and come up very rapidly in the modal month is somewhat characteristic of the relationship of gains to the other indices. All the gain curves show a rather prominent and limited range in which the mode may be selected. Gains are more closely related to birth weights than any of the other

indices, the correlations with birth weights in the 0 and -1 months being .75 and .70 respectively. The close relationship between the birth weights and the gains made by the same individuals, .70, but the fact that this correlation was not as high as that between the birth weights of young carried in utero during the last month of the gestation period and the gains made during the same month between birth and weaning by other individuals was noted. A high correlation, .60 was also maintained with fetuses carried in the first month of the gestation period when such gains were made. This tends to emphasize the similarity of reaction to environmental conditions, whether it be during intra- or extrauterine life. The correlation of gains to birth weights in the -2 and +2 months of .51 and .50 also indicates that the birth weights of the young are materially influenced by conditions before conception of the litter and that the influences on gains are not to be confined to that period after birth when the gains are made. The values of r in the +3 and -3 months which are .46 and .38 respectively contribute further support to this suggestion. Even in the -4 and -5 months the r values are .30 and .22, thus carrying some influence on birth weights back further than 6 months before birth. The time relations between gain and birth weights were discussed under birth weights and do not call for further comment.

The per cent raised of born alive show the next highest correlations with gain. It is of interest to note that approximately equal correlations are shown in the same month and in the first succeeding month which are .69 and .70 respectively. The other important correlation coefficients are in order of size in the -1 month, .54, in the

+2 month .51, in the -2 month .36, in the +3 month .33, and the -3 month .22. From the correlation curve it is quite apparent that the points of expression of maximum correlation of gain and per cent raised are close to 13 days apart. As the per cent raised is expressed later the influences must act 13 days earlier in the gestation period on per cent raised than on gains.

Gain is most closely correlated with size of litter in the +1, +2, and 0 months, with values for r of .69, .63, and .55. The values of r in the +3 and -1 months were .44 and .40, thus bringing out the closer relation between size of litter in succeeding months than in preceding months which is to be expected, since size of litter must be mainly determined 68 days before it is expressed, while gains are somewhat more of an immediate expression of conditions. The values of r for the -2, -3, -4, and -5 months are relatively low, being .28, .20, .08, and .04 respectively. From these values for r the mode of a smoothed curve would be expected to fall close to +30 days but just a little beyond when taking into account the higher value of r in the +2 month than in the 0 month. The mode was estimated at +34 days.

Per cent born alive in the 0 month shows a relatively high correlation, .62, with gains made in the same month with correlations of .55 for the -1 and .50 for the +1 months respectively. The correlation of gain with per cent born alive in the -2 and -3 months and +2 monthwere .41, .34, and .28. From the correlation curves it was estimated that the maximum relationships were expressed 8 days earlier for per cent born alive than for gains with the latter expressed at weaning and the former at birth.

Frequency of litter shows the lowest correlations with gains of any of the indices; only two values of r, .37 and .27, in the +1 and 0 months can be considered of importance, tho those in the -1 and +2 months, .21 and .20, fit well in the curve. The time relations between gains and frequency of litters do not call for further comment than was given under frequency of litter.

In general the birth weight curves were somewhat bimodal and flatter but did not begin as low as the gain curves, tho the curves for the latter form more distinct modes. The relation of birth weights to mortality was discussed earlier when the birth weights of the different litter sizes were presented in relation to fate, but the correlations bring out quite strikingly that this is not to be considered as a direct relation, since the correlations with the per cent born alive in the succeeding month and the per cent raised in the preceding and succeeding months are large.

The modal relation between the manifestation of characteristics showing maximum relations were with birth weights as a base at +29 days for frequency of litter, +45 days for size of litter, +14 days for gains, +12 days for per cent born alive and +25 days for per cent raised. The modes of the gain correlation curves were established at +20 days for frequency of litter, +34 days for size of litter, -14 days for birth weight, -8 days for per cent born alive and +13 days for per cent raised. The modal relation between birth weights and the other indices thus occurs from 9 to 20 days earlier than the modal relation between gains and the same indices. The weight curves bring out the similarity of the reaction of intra- and extrauterine life to the environment, but the birth weight and gain relationships with the other indices are distinctive in the relatively

greater tendency for the birth weights to be affected over a longer period, tho both bring out the necessity of proper preparation of the dam before conception, for maximum attainment in gain as well as birth weights.

Mortality.- In contrast with most of the curves for the correlations with birth weights the 9-months' period covers practically the entire time over which there are significant relationships for per cent born alive and per cent raised of those born alive with themselves and with the other indices. The curve for per cent born alive with itself is particularly steep and the significant relations cover about 5 months, i. e., 2 months in either direction from the 0 month. The significant relations between the per cent raised of born alive in successive months covers about 7 months, but the relation is dwindling out pretty rapidly 3 months away. The curves for the correlation of per cent born alive and per cent raised with the other characteristics are similar in shape and the values are quite uniform except that those for per cent raised are somewhat higher and the curves are broader. It is therefore not surprising that the correlations between the two should be relatively high, the maximum being .64 for the same litters, i. e. per cent born alive in the 0 month and per cent raised in the +1 month. A much lower correlation would have been considered reasonable as there might be some negative relation. If conditions were such that most of the young in a certain group were born alive and the relatively weak ones survived at birth it might be expected that mortality after birth would be greater. Evidently if conditions are favorable for low mortality at birth, a relatively large percentage survive to weaning. As will be

Table 19

Coefficients of correlation between per cent born alive in the zero month and the various monthly indices over a 9-months period

	Preceding and succeeding months									
	-4	-3	-2	-1	0	+1	+2	+3	+4	+5
Litters per 100 matings	-.614	+.065	+.051	+.198	+.298	+.397	+.156	+.135	+.070	
Size of litter	+.068	+.024	+.129	+.241	+.470	+.512	+.543	+.345	+.241	
Birth weights of raised	+.057	+.101	+.213	+.417	+.435	+.323	+.285	+.302	+.218	
Gain to weaning		+.131	+.279	+.504	+.618	+.551	+.412	+.344	+.223	+.113
Per cent born alive	+.055	+.086	+.300	+.476	+1.000	+.476	+.300	+.086	+.055	
Per cent raised of born alive		+.062	+.192	+.447	+.595	+.643	+.454	+.306	+.195	+.124
Net fertility	+.050	+.138	+.301	+.509	+.702	+.583	+.418	+.289	+.184	
Per cent males	+.056	+.054	-.018	-.118	-.230	-.044	-.012	+.023	+.061	

Table 20

Coefficients of correlation between per cent raised of born alive in the zero month and the various monthly indices over a 9-months period

	Preceding and succeeding months									
	-5	-4	-3	-2	-1	0	+1	+2	+3	+4
Litters per 100 matings	-.045	-.002	+.074	+.133	+.195	+.384	+.345	+.128	+.101	
Size of litter	+.014	+.095	+.185	+.315	+.428	+.594	+.591	+.488	+.345	
Birth weights of raised	+.153	+.176	+.306	+.462	+.538	+.500	+.409	+.319	+.319	
Gain to weaning		+.209	+.332	+.515	+.695	+.694	+.537	+.361	+.223	+.153
Per cent born alive	+.124	+.195	+.306	+.454	+.643	+.595	+.447	+.192	+.062	
Per cent raised of born alive		+.117	+.223	+.417	+.727	+1.000	+.727	+.417	+.223	+.117
Net fertility	+.061	+.159	+.312	+.511	+.706	+.724	+.562	+.328	+.211	
Per cent males	+.126	+.074	-.045	-.134	-.118	-.102	-.075	-.028	+.044	

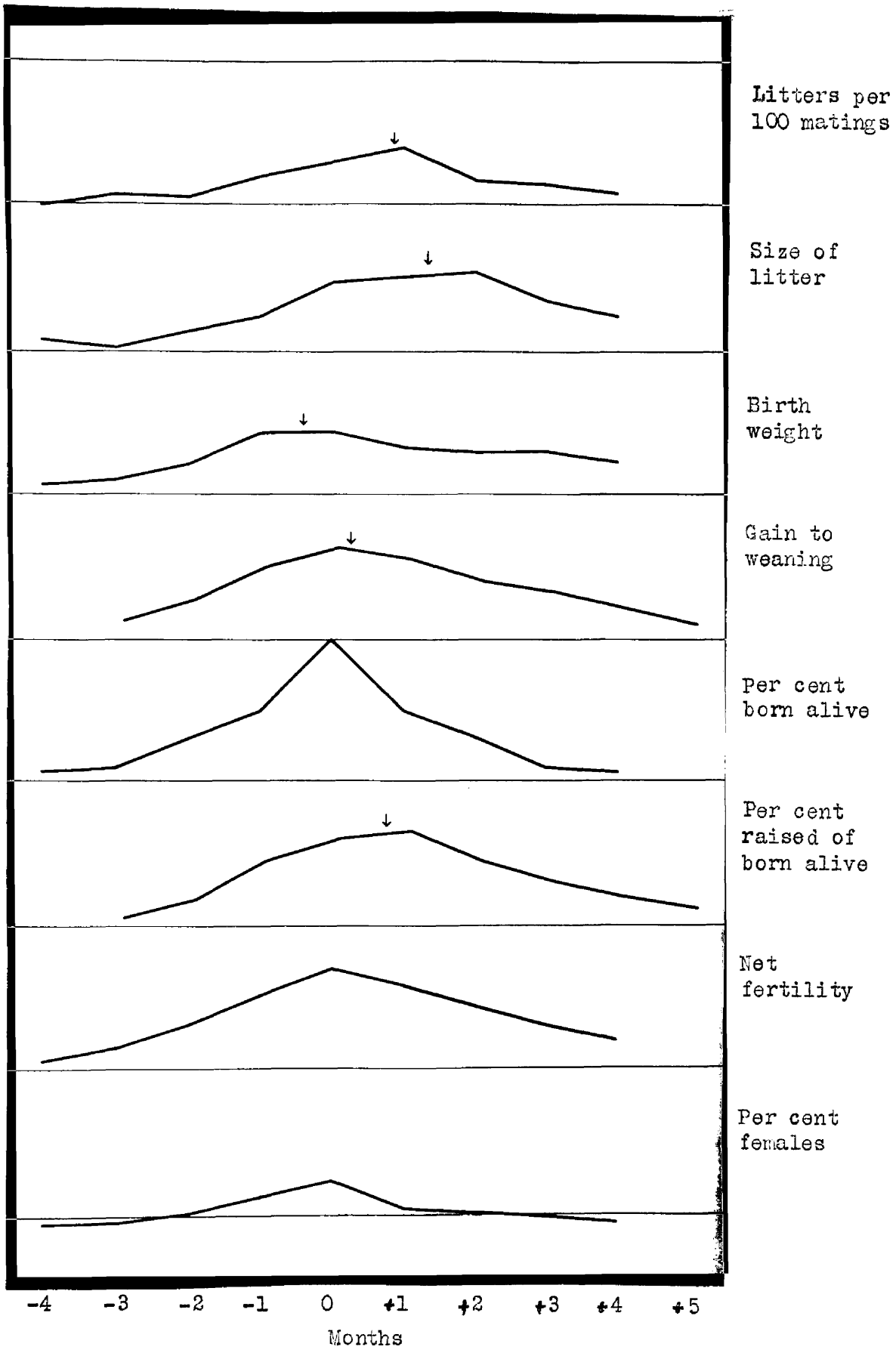
shown later the maximum influences on per cent raised as well as on per cent born alive operate before birth tho the one is not expressed until a month after birth and is modified by a month's extrauterine environmental conditions while the other is without the latter influence.

It is curious that per cent born alive is not as closely related to itself in successive months as it is to certain of the other indices in successive months. There are higher correlations for 2 months with per cent raised, 3 months with gains, and 2 months with size of litter. The correlations of per cent born alive separated by 2 months are .30, while those for 3 and 4 months apart are .09 and .06. This is quite obviously the most narrow peaked curve observed expressing relationships for any of the indices with themselves in successive months except for frequency of litter which shows no relation in successive months, but the explanation already given for the later characteristic shows that this is not necessarily a true expression of conditions.

Per cent born alive showed the closest correlation with per cent raised. The values of r for per cent raised in the +1 and 0 months were .64 and .59. The correlation in the +2 and -1 months were in each case .45 and in the +3, +4 and -2 months .31, .20, and .19 respectively. The other 2 months were below .12. These correlations show that per cent born alive is more closely related to per cent raised in the succeeding than in the preceding months, placing the influences on mortality between birth and weaning back in the gestation period. The mode of the curve must fall somewhere between +15 and +30 days and it was estimated taking into account the more distant values of r at +23 days.

Chart XVIII

Correlations between Per Cent Born Alive and Other Indices.



The correlations of per cent born alive and gains in proximate months are not quite so large as the correlation of per cent born alive with per cent raised in the similar months but the correlations are higher for a longer period between per cent born alive and gains, especially for gains in succeeding months. For gains in the 0, +1, and -1 months the correlations were .62, .55, and .50. Relatively high correlations .41 and .34 were also observed with gain in the 2nd and 3rd succeeding months (+2 and +3). The correlations with gains in the -2 and +4 months were likewise greater than three times their probable errors, .28 and .22, but in the -3 and +5 months the correlations were .13 and .11. The mode of the correlation curve must be very close to 0 but a little toward the + side. The point estimated was at +8 days. Again there is a relatively high relation between mortality at birth and the gains made by the same individuals, but here again the lag can not be attributed too heavily to a direct cause of it being the same individuals as it continues for the gains 2, 3, and even 4 months afterward. The time relations placing the expression of the concomitant influence on per cent born alive and gains 8 days apart indicates that the litters on which the gain was measured were born 25 days before those showing the influence on per cent born alive appeared. This relation has been more fully discussed under gain.

The correlations of per cent born alive with size of litter were highest in the +2, +1, and 0 months, .54, .51, and .47. For the size of litter in the +3, +4, and -1 months the correlations with per cent born alive were .35, .24, and .24. Other relations were not significant. The curve of the correlations between per cent born alive and size of litter presents as much of a problem in indicating the mode as any of

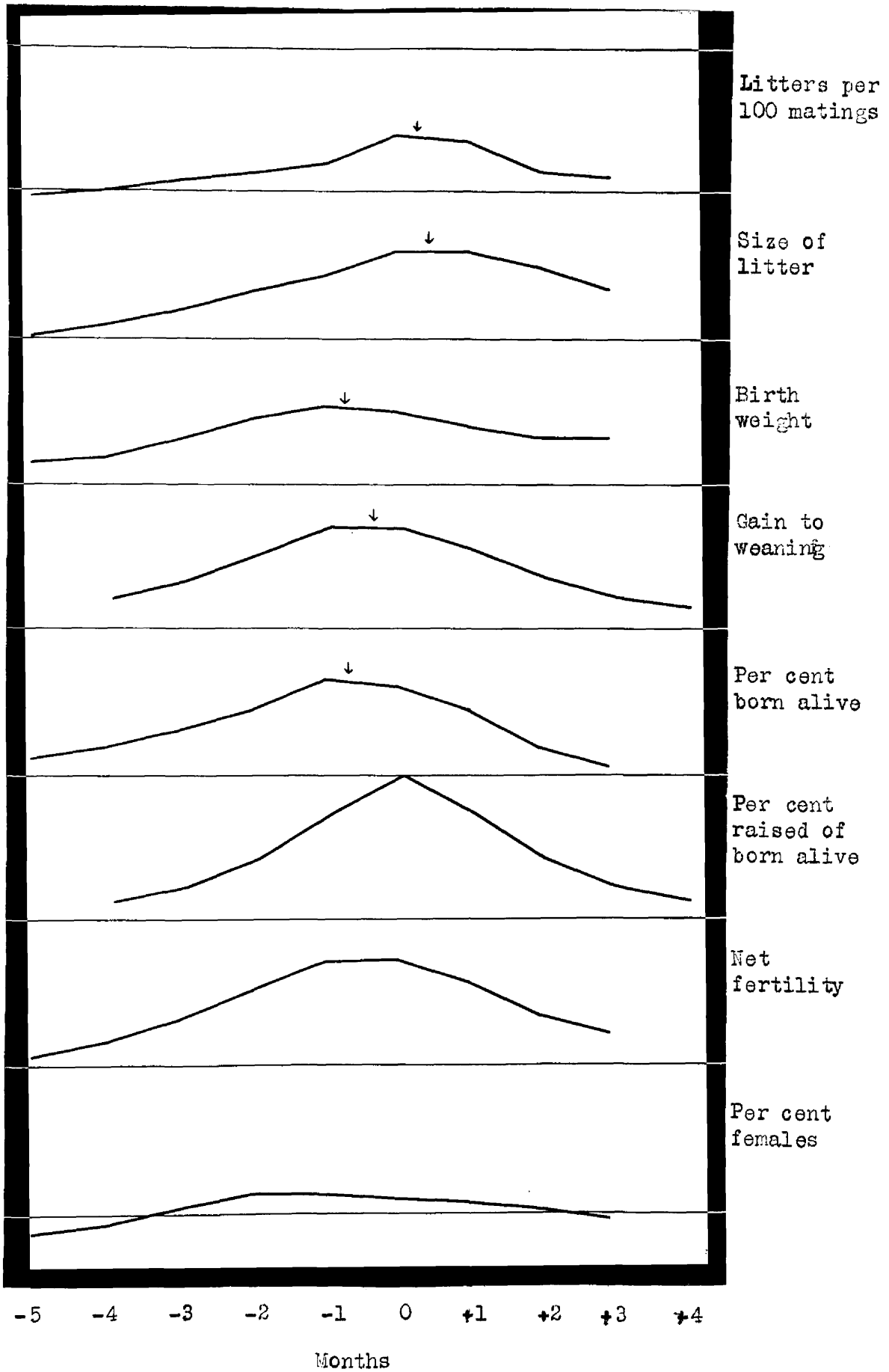
the curves that have been dealt with. It is very evident that the correlations in the +2, +1, and 0 months are much larger than the others and the mode must be somewhere between these and probably between +1 and +2 as the latter is the largest of the three values. The mode was estimated at +39 days. When the points from -3 to +4 were fitted by the formula for a 2nd order parabola the expression was $y = .436 + .072\ x - .029x^2$. When fitted in 3-day intervals this throws the mode at +39 days and since this had been previously arrived at by inspection it was accepted at this point. This relationship was discussed under size of litter.

Per cent born alive does not show any very high correlation with birth weights but significant relations extend over a relatively long period as was pointed out in the weight correlations. The correlations with birth weights in the 0 and -1 months were practically the same, .43 and .42, and in the +1 month .32. The +3 and +2 months were practically the same, .30 and .29, with the +4 and -2 months following closely at .22 and .21. The fact that the relations of per cent born alive with birth weight in successive months is very near the same simply bears out the tendency toward the bimodal characteristic of most of the birth weight curves which has been previously referred to. The time relations have likewise been discussed in which it was pointed out that those litters showing the greatest relation of birth weight to per cent born alive were born 12 days before those from which per cent born alive was measured were born.

Per cent born alive shows a correlation of .40 with litters per 100 matings in the +1 month, .30 in the 0 month, and .20 in the -1 month.

Chart XIX

Correlations between Per Cent Raised of Born Alive and Other Indices



The other values were low but in the succeeding months they were somewhat higher than in the preceding months. The time relations have been previously noted showing a 26 day interval between the expression of greatest associated variation from which it was pointed out that the influence on the 2 characteristics must act on per cent born alive at least as early as the 26th day of gestation.

The relations of per cent raised of born alive to the other indices generally extend over a somewhat longer period than the correlations of per cent born alive and these indices. Likewise significant correlations of per cent raised in successive months extend over a considerably longer period. The values for r, 1, 2, 3, and 4 months away were .73, .42, .22, and .12.

The closest relation of per cent raised to other indices is with gains in the -1 and 0 months with correlations of .70 and .69 and with gains in the +1 and -2 months .54 and .51. The correlations of per cent raised with gains in the more distant months are just a little higher for the preceding than for succeeding months the same distance from 0. In the +2 month r equals .36, in the -3 month the value is .33 and in the +3 month the correlation coefficient is .22. The values in the -4 and +4 months are .21 and .15.

The time interval between expressions of maximum relation of per cent raised and gain have been previously discussed under gain. It is sufficient to say that here we have an almost symmetrical curve with equal correlations in the 0 and -1 months and taking into account the higher correlation in + months, the mode is placed at -13 days.

The correlations of per cent raised to per cent born alive have been previously discussed under the latter heading. The highest correlation is in the -1 month, .64, followed closely by .59 for the 0 month. As in case of the correlations of per cent raised with gains the correlations of per cent raised with per cent born alive are somewhat higher in preceding than in succeeding months. The values of r with per cent born alive in the -2 and +1 months are in both cases .45, and the -3 and -4 months, .31 and .20. The mode of the curve was placed at -23 days.

Per cent raised was equally correlated with size of litter in the 0 and +1 months, .59. The correlation in the +2 month, .49, was comparable to r in the -1 month, .43, as were the .34 in the +3 month and .32 in the -2 month. The mode for the curve was estimated at +10 days. Thus the maximum association in size of litter and per cent raised was between those born 43 days apart.

Per cent raised showed the closest relation with birth weights in the -1 and 0 months, the values of r being .54 and .50, with values in the -2 and +1 months of .46 and .41. The other correlations with birth weights in the more distant months continued relatively high, i. e., in the +3 and +2 months .32, in the -3 and -4 months, .31 and .18. This is simply an expression of the flatness of all the birth weight curves. In this case the bimodal tendency is not so pronounced as in many of the birth weight curves tho there is a slight indication of it.

Birth weights is the third of the indices which in the -1 and 0 months show maximum and approximately equal relations with per cent raised, gains and per cent born alive being the other two. In each of

the three cases the correlation in the -1 month is slightly greater than in the 0 month.

The mode of the curve for the correlations between per cent raised and birth weights might be estimated as falling anywhere over a considerable period, but it would be expected to fall near -30 days. However, taking into account the relatively higher values in succeeding than in preceding months, it was estimated at -25 days.

The correlations of per cent raised with frequency of litter are again low as is characteristic of the relation of frequency of litter to the other indices. In order of the months they are quite similar to size of litter and in both cases the largest values of r appear in the 0 and +1 months, being .38 and .34. These of course are much smaller than the correlations with size of litter. The only other significant correlation is .19 for per cent raised with frequency in the -1 month. Though the correlations are low, the time relations are quite definite as between 0 and +30 days and because of the larger correlation in the zero month the mode should be much less than 15 days. As discussed under frequency of litter this was placed at +5 days.

It has been pointed out that the correlations with per cent born alive formed narrower peaked curves than the correlations with per cent raised tho the correlations with the latter in the months of maximum relation were frequently a little larger. The difference between the expression of the modes of the per cent born alive and per cent raised curves when related to each other was 23 days. If all of the indices were associated with the expression of the same factors it would be expected that the difference between the mode of the per cent born alive -

frequency of litter, and per cent raised - frequency of litter correlation curves, etc., would show a similar difference. Such is closely approached. The modes for the different index correlation curves with per cent born alive and per cent raised were respectively: frequency of litter +26 and +5 days, size of litter +39 and +10 days, birth weights -12 and -25 days and gains +8 and -13 days. The differences thus range from 13 to 29 days.

Net fertility.- The number of young born during the month which are raised to weaning age per 100 pairs mated has been taken as the measure of net fertility. It is quite obvious that this is simply the product of the litters per 100 matings, size of litter, per cent born alive, and per cent raised of born alive, four indices which were discussed above. Net fertility is necessarily very closely related mathematically to all these characteristics, the correlation coefficients calculated being .70 or more in all four cases. (Table 21) It is, however, interesting to note that there are other correlations nearly as great in other months. For example, the coefficient of correlation with per cent raised in the following month, .71, is practically as large as the correlation with the data forming a direct component of it. The correlations with gains made during the month that the young are being raised and during the gestation period, particularly the last month, are nearly as large as the correlation between net fertility and other indices forming component parts of it. The correlations with the size of litter for the first two months after the young are born are .65 and .61; in fact, frequency of litter is the only one of the fertility or weight factors which does not show a rela-

Table 21

Coefficients of correlation between net fertility in the zero month and the various monthly indices over a 9-months period

	Preceding and succeeding months									
	-4	-3	-2	-1	0	+1	+2	+3	+4	+5
Litters per 100 matings	+.034	+.166	+.192	+.173	+.718	+.268	+.259	+.179	+.117	
Size of litter	+.155	+.217	+.271	+.440	+.743	+.658	+.611	+.415	+.355	
Birth weights of raised	+.146	+.217	+.401	+.509	+.518	+.388	+.314	+.326	+.246	
Gain to weaning		+.235	+.470	+.669	+.684	+.601	+.439	+.276	+.189	+.061
Per cent born alive	+.184	+.289	+.418	+.583	+.702	+.509	+.301	+.138	+.050	
Per cent raised of born alive		+.211	+.328	+.562	+.724	+.706	+.511	+.312	+.159	+.061
Net fertility	+.203	+.337	+.486	+.616	+1.000	+.616	+.486	+.337	+.203	
Per cent males	+.074	-.098	-.062	-.155	-.167	-.102	-.040	+.008	+.015	

tively high correlation for several months before and after the 0 month. The correlations of frequency of litter to net fertility jump up from .17 in the -1 month to .72 in the 0 month and down to .27 in the +1 month. Two months earlier gains and per cent raised show correlations of .47 and .33 and birth weights and per cent born alive of .40 and .42 respectively. It has been brought out above that these conditions are somewhat dependent upon intrauterine life and therefore must have been operative prior to that time. This merely substantiates what was mentioned in regard to the lack of relation of frequency of litter in one month to frequency in preceding or succeeding months. The difficulty of getting litters has often been observed as one of the important drawbacks to the production of larger numbers of young in guinea pigs, and the data clearly point toward this as an important factor. Evidently females are not breeding at the first oestrus period after parturition to any great extent or higher correlations would be obtained between the 0 and the second or third months away. Further attempt is not made to discuss the correlations between net fertility and the other indices, especially as concerns time relations, because net fertility can not be confined to a particular month or a particular time.

Sex Ratio.- Attention has already been called to the fluctuations in the sex ratio and the indication that such might be related to the seasons and possibly to variations in the other monthly indices. (See Charts XII and XIII).

When planning the monthly indices in the course of the study the sex ratio was tabulated as a matter of interest but with the expecta-

tion that no correlation would be found with any of the other indices. However, amongst the correlations as a whole nearly all were positive, but of the 63 correlation coefficients between per cent males and the other indices given in Table 22 there were only 17 which were positive, and all of these were with indices three months or more distant from the month in which the sex ratio was measured. Twelve were at the extreme end of the period and all were small. The other positive correlations in the +5 month for gains and per cent raised and in the +4 month for frequency of litter were .10, .13, and .11, respectively. Though the majority of the correlations between the sex ratio and the other characteristics were negative, they were all relatively small; there is, however, at least one month in which the correlation of the sex ratio with each of the other indices is -.12 or larger. With litters per 100 matings the alternation of the months in the degree of relationship is very distinct. The correlation of sex ratio in one month and frequency of litter in the next month was -.13; with sex ratio in one month and frequency in the third following month -.20. The correlation of per cent of males in one month with size of litter in the same month and in the three succeeding months were -.11, -.08, -.16, and -.12, respectively. The correlations with birth weights in the same and in the preceding months were both -.12 and in the succeeding month -.09. The relation to gains covers a similar period except that the correlations were somewhat higher, being -.11, -.12, -.16, and -.10 in the second month later. There are no possible significant correlations with per cent born alive except in the same month which is the highest of the coefficients in this group, -.23, and in the next fol-

Table 22

Coefficients of correlation between per cent of males in the zero month and the various monthly indices over a 9-months period

	Preceding and succeeding months									
	-4	-3	-2	-1	0	+1	+2	+3	+4	+5
Litters per 100 matings	+.054	-.008	-.032	-.128	-.048	-.130	-.017	-.196	+.107	
Size of litter	-.069	+.009	-.019	-.020	-.113	-.082	-.159	-.124	-.073	
Birth weights of raised	+.023	-.009	-.016	-.118	-.119	-.094	-.083	-.063	+.008	
Gain to weaning		+.017	-.064	-.108	-.121	-.162	-.103	-.012	-.003	+.101
Per cent born alive	+.061	+.023	-.012	-.044	-.230	-.118	-.018	+.054	+.056	
Per cent raised of born alive		+.044	-.028	-.075	-.102	-.118	-.134	-.045	+.074	+.126
Net fertility	+.015	+.008	-.040	-.102	-.167	-.155	-.062	-.098	+.074	
Per cent males	+.076	-.102	+.008	+.047	+1.000	+.047	+.008	-.102	+.076	

lowing month, -.12. The three highest correlations with per cent raised are within the same month and during the first and second succeeding months, being -.10, -.12, and -.13, respectively.

Very little would be thought of the small correlations of per cent males with the other indices if they were not so uniform and all in the same direction, thus, all indicating that a lower percentage of males is associated with all other indices which are assumed to result from favorable conditions. Per cent born alive showed the largest correlation with sex ratio which is hard to understand when sex was found to be unrelated to mortality at birth. In the different litter sizes the values for the per cent born alive alternated for the sex ratio and the per cent of the two sexes born alive was practically the same.

It is hard to understand how environmental conditions could have any direct effect upon sex ratio. The customary explanation for modification of sex ratios as affected by environmental conditions is to assume a differential mortality of the sexes. This would point toward sex reversal, a greater prenatal mortality of females with unfavorable conditions which is wholly contrary to the generally accepted ideas of the differential mortality of the sexes prior to birth or a decreased mortality of males in favorable seasons. If the latter explanation be accepted it assumes a preponderance of males in the primary sex ratio. Riddle (1927) discussed the greater prenatal mortality generally found in males and relates it to the fact that while in utero males are subjected, to their detriment, to the female secretions of the dam, while intrauterine environment is more favorable for the same reason for females. In the very valuable and carefully conducted studies by the same author in pigeons in which sex is related to the rate of metabolism

which has in turn been tied up with the endocrine secretions, particularly of the thyroid glands, the results of which are largely summarized by Riddle (1928), it has been found that there is a preponderance of males hatched from eggs produced in the winter and early spring. The case in birds where all ova having a possibility of development may be identified is somewhat different than in mammals where only those embryos reaching birth and which are not eaten by the dam are found.

It should be understood that the sex ratio refers to all young born and therefore if there is a greater mortality it must occur at such a young age that sex can not be determined or so that resorption or maceration has advanced to such a point that the sex can no longer be identified or the young found at birth. There were only 391 young recorded for which sex was not known. This includes abortions and macerated young and cases where the dams had eaten sufficient portions of the young so that sex identity was uncertain. It is doubtful if this slightly over 1 per cent of the numbers could have accounted for the relationship had they all been of one sex.

The primary (conception) sex ratio has been estimated by various means with somewhat different conclusions. Crew (1925-26) concluded from herd book data and the sex ratio of foetuses that the primary sex ratio in swine showed a larger percentage of males, while MacDowell and Lord (1926) concluded that the primary sex ratio in mice was equal. In Parkes' (1926) compilation of the sex ratio in mammals he assumed equality of the sexes at conception. This publication makes no reference to guinea pigs.

If equality of the sexes is assumed at conception the association between the sex ratio and the other indices may be explained either by

sex reversal or by greater mortality of females or reduced mortality of males when conditions for the other indices are favorable and vice versa. The sex reversal idea would possibly have some basis in Riddle's metabolic theory of sex determination but the second suggestion seems more tenable. It is generally recognized that there is more or less foetal mortality at all times and association with the season or environmental conditions of variations of the amount in the two sexes seems plausible.

In further study of the problem the relative relation between different indices was attacked from the standpoint of partial correlations. The partial correlation coefficients between per cent males and per cent born alive, eliminating the effect of per cent raised, size of litter and frequency of litter, were respectively -.20, -.21 and -.21. The partial correlation coefficients pointed toward per cent born alive as the most important relation. The other indices showed similar relations with per cent born alive and smaller correlations with sex ratio, and therefore they would not show further influence on it. Another mode of attacking this problem was by multiple correlations to see how much the coefficient was raised by including the influence of all the indices within the 0 month. Using the highest correlation with all seven other indices the multiple correlation with per cent males was .2486, which is not significantly different than the .2303 calculated for the simple correlation between per cent males and per cent born alive.

The net result of the total determination of sex ratio by the seven indices in the single month showing the highest correlations was 6.18 per cent, which is of course very small. Thus approximately 94

per cent of the variability in the sex ratio is not associated with the 7 indices in their month of maximum relation. This might be interpreted as indicating a strong tendency for some other definite means of sex determination, i. e., the chromosome theory, with a possibility of a slight influence of other conditions associated with the per cent born alive on sex.

Discussion.- The correlations between the indices ranged in the modal months in most cases from .40 to .75, indicating from 16 to 56 per cent association in the variations. These are obviously high for biological data so pronouncedly influenced by environmental fluctuations, and particularly when there appears to be an almost complete lack of cause effect relationship. The curves showed a dwindling of the degree of correlation as the time interval increased, tho in many cases the 9 months period employed was not sufficient to get away from a considerable association.

One of the first questions for consideration in discussing the correlations over the nine months period is: Are the relations between the different pairs of indices due to the same combination of environmental conditions or is the correlation between one pair of indices due to one set of conditions and the correlation between another pair due to a wholly different set of conditions? In order to bring this out clearly Chart XX has been constructed showing diagrammatically the interval between the reaction of each pair of indices to a common influence. The number of days interval between the evidence of the maximum relations are indicated. Straight lines show the shortest period between such expressions and angles show the longer intervals; for example: frequency

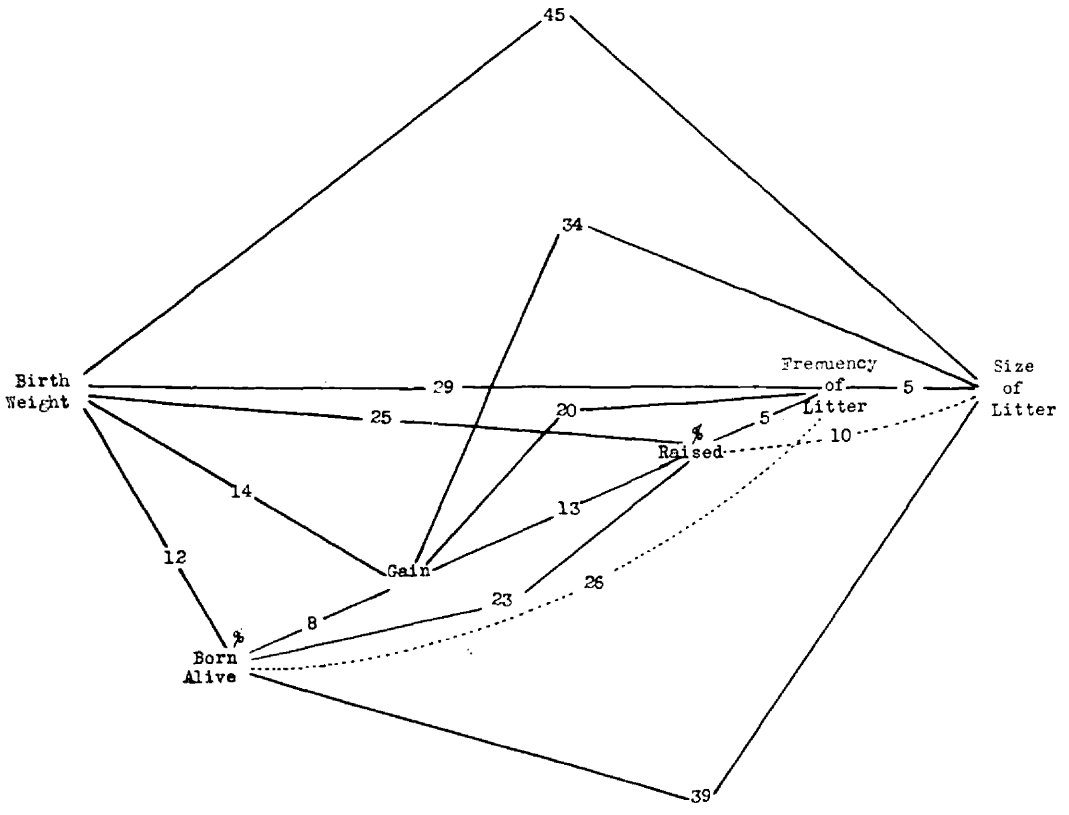
of litter is manifested 5 days before size of litter and birth weight 29 days before frequency of litter, but birth weight is evidenced 45 days before size of litter instead of 34 days before it. This is, however, the greatest discrepancy, other differences being between 11 days and complete agreement. Dotted lines have been used in the chart where the total is the same as the sum of the component intervals; for example: frequency of litters is evidenced 5 days before size of litter, per cent raised 5 days before frequency of litters, and per cent raised is 10 days before size of litter, and the last are thus connected by a dotted line.

There is in general close agreement between the different paths for measuring the time of evidencing frequency of litter, per cent raised, gain and per cent born alive, and between frequency of litter, per cent raised and birth weights, as well as between size of litter, frequency of litter and per cent raised; and per cent raised, gain, and birth weights. From the fact that limited groups can be selected which show similar relations and there are no very wide departures from the sum of any paths which may be followed, it is convenient to discuss these variations as tho all indices reacted to the same complex of conditions. Such are probably closely associated conditions but would not be expected to be identical.

Another question of interest is what is the order in which different indices evidence the effects of changed environmental conditions? The data throw light on this question only from the standpoint of associated variation in pairs of indices and do not contribute to the variations in a particular index resulting from a specific influence acting only on that index and having no influence or to a minor degree on other indices studied. The time intervals between the expression

Chart XX

Interval in Days Between Maximum Correlations



of the maximum amounts of concomitant variation in the different indices permits the establishment of the order in which the reactions are expressed with considerable certainty. The order of reaction to a particular stimulus is evident first in birth weights, second in per cent born alive, third in gains, fourth in per cent raised, fifth in frequency of litters and sixth in size of litter. This order is maintained for all the indices when considered with reference to any single one but there is slight overlapping when considered in relation to several. For example: variations in birth weights associated with frequency of litter are evidenced 29 days before frequency of litter and size of litter 5 days after frequency of litter; but variations in per cent born alive associated with variations in size of litter are evidenced 39 days apart, placing the expression of per cent born alive before birth weights when the latter is calculated from its relation to frequency of litter, and the former from its relation to size of litter. When birth weight is considered from its direct relation to size of litter it again evidences its variation associated with size of litter before the variations in per cent born alive are apparent.

Having established the relation between the time of expression of the associated variation in the different indices it becomes of considerable practical interest to know at what stage in the life history of the animal variations in the different indices are most likely to be effected. The most promising lead to this is in a consideration of the relation of the various indices to size and frequency of litter. Obviously these two indices must be mainly influenced before conception but there appears to be no way of determining just how long before conception from the data. The fa ct that size of litter requires 5 days

longer to react to certain conditions than frequency of litter helps, but it is not certain that frequency of litter responds immediately, nor is it to be expected that it should. For the want of a better starting point it may be assumed that frequency of litter is affected at conception and size of litter 5 days before conception. McKenzie (1926) found in swine particularly rapid growth of the follicles during proestrum with the elimination of some follicles at all times, which lends some support to the selection of such a base, and it is reasonable to believe that the elimination of follicles might be closely associated with environmental conditions.

Assuming that influences must act on size of litter 5 days before conception, we may estimate the time when the influences act on the other indices. The common influences between size of litter and birth weights would act on birth weights 28 days before birth, or at the 40th day of the gestation period for birth weight. On the other hand common influences between frequency of litter and birth weights act on birth weights at the 29th day of gestation. Similarly common influences on frequency of litter and per cent born alive act on the latter at the 26th day of gestation while with size of litter the action is placed at the 34th day of gestation. Common influences between frequency of litter and gain act on the latter at 15 days before birth or at the 53rd day of gestation and when calculated from size of litter at 6 days before birth or at the 62nd day of gestation. The time of influence on per cent raised is placed at the 38th day of gestation from its relation to both size of litter and frequency of litters.

The other four indices may now be considered with reference to the time in the gestation period between the action on each. There is 25 days difference in the expression of per cent raised and birth weights. Allowing for the expression of the former at weaning and the latter at birth this makes per cent raised influenced 33 - 25 = 8 days later in the gestation period than birth weights. Similarly gains are influenced 13 days later in the gestation period than per cent raised, 25 days later than per cent born alive, and 19 days later than birth weights. These intervals do not give any indication of the time in the life cycle of the animal or the duration of time between the change in the environment and the evidence of a reaction of a particular index to it. A three fold relation between two indices and the relation of the basic one to size of litters furnishes an indication of this but offers some complications. For example, birth weight was estimated to be influenced at the 40th day of gestation from its relation to size of litter, but at the 29th day of gestation from its relation to frequency of litter. When birth weight is used as the base calculated from its relation to size of litter, frequency of litter must be influenced 11 days after conception, which seems highly improbable. Similarly when gain, per cent born alive and per cent raised were employed as the basesand when the influences acting on them were calculated from size of litter, frequency of litter was influenced 9, 8 and 5 days respectively after conception. Notwithstanding this difficulty, the stage in the gestation period when each index was estimated to be influenced as calculated from the different indices gave fair agreement for the time between the expression of pairs of indices. The stage in the gestation period when maximum influences were estimated to act on each index from the

different bases were as follows:

Base	Stage of Gestation when Influence on Indices Occurred.					
	Frequency of litter	Size of litter	Birth weight	Gain	Per cent born alive	Per cent raised of born alive
	days	days	days	days	days	days
Frequency of litter		-5	29	53	26	38
Size of litter	Conception		40	62	34	38
Birth weight	11	-5		59	28	48
Gain	9	-5	43		37	49
Per cent born alive	8	-5	46	59		44
Per cent raised	5	-5	30	51	28	
Mean	6.6	-5	37.6	56.8	30.6	43.4

The mean values given in the last line show that the bases used indicated that frequency of litter was influenced at 6.6 days in the gestation period. Allowing for this, 6.6 days may be subtracted from the mean for the other indices. It may thus be estimated that the maximum influences on the different indices are not exerted later than about 12 days before conception for size of litter, the 31st day of gestation for birth weight, 50th day of gestation for gain, 24th day of gestation for per cent born alive, and 37th day of gestation for per cent raised of born alive.

From the estimates of the stage in the gestation period when the influences are most effective one may calculate the time intervening between an environmental influence and the evidence of its effect on the different indices. For instance, birth weights express the action of a particular condition which occurred about 37 days before. Similarly the other indices react to changed conditions approximately as

follows: per cent born alive 44 days, gains 51 days, per cent raised of born alive 64 days, frequency of litter 68 days, and size of litter 80 days after the exceptional condition occurred.

The time of operation has been referred to as if it were specific but the breadth of the correlation curves indicates that the influencing conditions extend over a considerable period and are more cumulative than immediate, some more so than others. Judging from the curves, frequency of litters and per cent born alive are more affected by immediate conditions than the others, with size of litter showing the next greatest tendency in this direction. The specific time mentioned should be taken as the latest point at which the maximum influences occur. It is probable that size of litter and frequency of litter react to influences earlier than those used as a basis. However, Loeb (1923) showed that there were no large follicles in the guinea pig ovary after oestrum and therefore frequency and size of litter would be expected to be the result of conditions acting some time during the 17 day period prior to the next ovulation. Papanicolaou (1924) found that ovogenesis in the guinea pig was going on at all times and that the rate was stimulated by favorable nutrition, seasonal conditions and oestral activity and retarded but not stopped by the presence of corpora lutea and competition in the ovary. These findings have a definite bearing on the estimate of the time when the frequency and size of litters might be influenced, and indicate that the time selected is within the limits of expectation.

For further solution of the time of operation of the various factors, controlled experiments are needed for the determination of specifically

what influences act on each index and how and when each acts. There is no doubt that it takes several days if not weeks or months in particular cases for conditions to effect a dam's physiological condition so that she will ovulate and conceive, whereas the time relations have been based on this as an immediate effect. Further, size of litter is no doubt effected at least by the beginning of the cycle, culminating in ovulation and the conception of the litter. The constant elimination of follicles from the ovary thruout the various stages in development has been cited by several authors. It thus appears to be a cumulative process tho there may be crucial periods with heavy elimination or times beyond which further atresia is a minor matter. The operation of such influences during the preceding period with an ovulation period intervening would not seem unreasonable.

If seasonal variations in the sex ratio are admitted, of which there seems to be considerable evidence, these variations must be associated with conditions other than those causing the variations in the other indices with the possible exception of per cent born alive; a sex difference in the prenatal mortality at an early stage in gestation being the most plausible means by which the variation in the sex ratio could be brought about.

Effect of Parity on Indices.

In making the original tabulations the individual cards were sorted and tabulated three times, once by months and year, once by year, and once by parity, i. e., order of litters, and the totals in

each litter size and sex checked. The tabulation by parity showed some interesting and rather striking relationships. Tables 23 and 24 show the numbers of individuals and litters born in the first, second, third, etc., litters of dams as well as the averages for each parity for size of litter, sex ratio, mortality, weights and gains. The numbers decrease from 2,980 litters born in first parities to two litters each in the fifteenth and sixteenth parities. The small numbers in the litters beyond the tenth make the data for the eleventh to sixteenth parities of doubtful significance.

For all factors, except birth weights of born dead and died, the second, third, and fourth litters of dams were generally superior to first litters and litters after the fifth. The differences are so uniform for all indices that some importance should be given to parity as a factor affecting size of litter, weights, and mortality. It is recognized that the age at which first litters are born varies considerably, and the matter of age and maturity may be more important than that of parity, tho Wright (1926) found a correlation of .927 ± .002 between age of dam and parity in Family 35. An opportunity to study the influence of the correction factors for size of litter and sex on weights and mortality is also given with the data for each parity as both corrected and uncorrected averages are presented in the tables. The effect of the correction factors is much the same as was mentioned for the indices in the combined months, and the explanation of the differences between the corrected and uncorrected values are quite obvious and do not call for further comment.

Table 23

Averages for Fertility Characters According to Parity (Litters 1 to 6)

Parity	Litters	Individuals	Size of litter	Sex ratio	Born alive		Raised of born alive	
					Corrected	Uncorrected	Corrected	Uncorrected
	Number	Number	Number		Per cent	Per cent	Per cent	Per cent
First	2,980	7,108	2.39	51.42	81.69	83.60	82.20	82.94
Second	2,548	6,891	2.70	51.16	83.54	82.80	84.26	83.91
Third	2,146	5,853	2.73	50.33	85.40	84.38	84.32	83.93
Fourth	1,620	4,442	2.74	49.73	84.77	83.42	82.70	82.20
Fifth	945	2,380	2.52	49.57	82.55	82.72	78.63	78.75
Sixth	629	1,562	2.48	50.68	79.38	79.86	78.41	78.68
Seventh	425	1,029	2.42	48.13	81.13	81.89	78.27	78.61
Eighth	278	638	2.29	48.55	78.67	80.32	78.71	79.32
Ninth	163	385	2.36	53.05	79.26	79.84	78.17	78.41
Tenth	91	209	2.30	49.76	79.94	81.46	72.57	73.05
Eleventh	56	114	2.04	60.71	65.50	66.96	66.11	66.67
Twelfth	25	52	2.08	38.00	78.06	80.00	64.30	65.00
Thirteenth	10	19	1.90	56.25	53.69	56.25	98.22	100.00
Fourteenth	3	8	2.67	50.00	59.88	62.50	98.20	100.00
Fifteenth	2	4	2.00	50.00	73.25	75.00	66.33	66.67
Sixteenth	2	6	3.00	50.00	48.17	50.00	65.67	66.67
Average	11,923[1]	30,700[1]	2.57	50.58	83.01	83.01	82.30	82.30

[1]Total not average.

Table 24

Averages for Birth and Weaning Weights and Gains According to Parity (Litters 1 to 6)

Parity	Birth weights						Weaning weights		Gain to weaning	
	Born dead		Died		Raised					
	Corrected	Uncorrected	Corrected	Uncorrected	Corrected	Uncorrected	Corrected	Uncorrected	Corrected	Uncorrected
First	61.40	62.87	69.46	72.24	79.53	81.98	221.90	226.61	142.37	144.63
Second	61.60	59.81	69.00	68.60	81.21	80.02	227.07	224.24	145.86	144.22
Third	63.78	62.62	71.38	69.71	81.97	80.43	229.53	226.17	147.56	145.74
Fourth	64.36	62.96	69.87	67.82	82.24	80.42	225.63	221.90	143.39	141.48
Fifth	65.60	66.47	71.85	70.99	81.03	81.74	222.29	223.58	141.26	141.84
Sixth	64.04	64.68	71.51	71.05	80.44	81.75	216.09	218.66	135.65	136.91
Seventh	64.14	66.57	71.41	72.24	81.29	82.82	222.58	225.54	141.29	142.72
Eighth	67.86	74.04	71.51	73.61	80.95	84.34	220.37	226.93	139.42	142.59
Ninth	66.96	72.81	68.33	68.38	79.71	81.29	208.86	212.54	129.15	131.25
Tenth	68.56	75.76	71.25	71.58	78.03	80.93	213.47	218.80	135.44	137.87
Eleventh	66.43	74.91	74.46	80.56	75.84	80.30	211.89	220.22	136.05	139.92
Twelfth	62.87	61.00	70.52	74.64	78.86	84.23	202.64	213.15	123.78	128.92
Thirteenth	73.51	94.00	-----	-----	79.84	83.56	174.28	180.56	94.44	97.00
Foufteenth	79.45	80.00	-----	-----	78.41	79.40	249.53	252.20	171.12	172.80
Fifteenth	64.23	64.00	65.87	65.00	78.96	91.50	231.45	251.50	152.49	160.00
Sixteenth	79.89	80.67	67.90	67.00	78.75	76.50	218.38	213.50	139.63	137.00
Average	63.25	63.32	70.27	70.24	81.01	81.03	224.62	224.42	143.61	143.39

Table 25

Differences in successive parities

Parity	Size of litter	Per cent born alive	Per cent raised	Birth weights of raised	Weaning weight	Gain
First and second	+.31 ± .019	+1.85 ± 0.432	+2.06 ± 0.469	+1.68 ± 0.188	+5.17 ± 0.685	+3.49 ± .587
Second and third	+.03 ± .023	+1.86 ± 0.434	+0.06 ± 0.479	+0.76 ± 0.196	+2.46 ± 0.714	+1.70 ± .611
Third and fourth	+.01 ± .026	-0.63 ± 0.479	-1.62 ± 0.548	+0.27 ± 0.220	-3.90 ± 0.801	-4.17 ± .686
Fourth and fifth	-.22 ± .030	-2.22 ± 0.639	-4.07 ± 0.756	-1.21 ± 0.288	-3.34 ± 1.000	-2.13 ± .898
Fifth and sixth	-.04 ± .038	-3.17 ± 0.868	-0.22 ± 1.011	-0.59 ± 0.378	-6.20 ± 1.236	-5.61 ± 1.176
Sixth and seventh	-.06 ± .045	+1.75 ± 1.075	-0.14 ± 1.248	+0.85 ± 0.465	+6.49 ± 1.692	+5.64 ± 1.449
Seventh and eighth	-.13 ± .052	-2.46 ± 1.336	+0.44 ± 1.570	-0.34 ± 0.585	-2.21 ± 2.128	-1.87 ± 1.823
Eighth and ninth	+.07 ± .067	+0.59 ± 1.746	-0.54 ± 2.028	-1.24 ± 0.756	-11.51 ± 2.748	-10.27 ± 2.354
Ninth and tenth	-.06 ± .085	+0.68 ± 2.331	-5.60 ± 2.828	-1.68 ± 1.024	+4.61 ± 3.724	+6.29 ± 3.190
Tenth and eleventh	-.26 ± .100	-14.44 ± 3.537	-6.46 ± 4.360	-2.19 ± 1.542	-1.58 ± 5.608	+0.61 ± 4.804
Eleventh and twelfth	+.04 ± .157	+12.56 ± 4.899	-1.81 ± 6.300	+3.02 ± 2.221	-9.25 ± 8.077	-12.27 ± 6.918

Table 25 gives the differences between the average indices for successive parities from 1 to 12, together with their probable errors.

The probable errors for size of litter were calculated for each parity by the usual formula P. E. = .6745 $\frac{\sigma}{\sqrt{n}}$ where σ is the standard deviation for the size of litter and n is the number of litters in each parity. The differences for the fates and weights were calculated from the values corrected to eliminate the effect of litter size, which is in accord with the way the other data were treated, and it is believed by eliminating this effect the influence of parity is brought out more clearly without the complication resulting from differences in the size of litters. Differences in the birth weights were only recorded for those which were raised as such are not subject to the wide variations and complicated by abortions which can not always be distinguished. The standard deviation for the weights was not determined but the values given by Wright (1922) based on some of the same animals were used as follows:

Birth weight of raised (litter size constant) 13.62 gm.

Weaning weight (litter size constant) 49.53 gm.

Gain to weaning (litter size constant) 42.42 gm.

Slight differences in the standard deviations which might be found by calculating the constant from the complete data could not materially affect the results where n is as large as in the earlier parities.

The probable errors of per cent born alive and per cent raised were calculated from the corrected values by the usual formula for percent-

ages, P. E. = $.6745\sqrt{\frac{P\ (1-P)}{n}}$ in which P is the per cent born alive or raised. For per cent born alive n was the number of individuals born and for per cent raised n was the number of individuals born alive. Wright (1922) has raised some question as to whether in the above formulas n should represent the number of individuals or the number of litters and has suggested increasing the probable error by 25 per cent to offset this uncertainty. It seems simpler to consider differences of 3.75 or better 4 times the probable error as the point where significant differences are indicated instead of the common point of 3 times as indicating chances of 21 to 1. The 25 per cent limit was selected empirically and the choice of 4 times the probable error is as logical and allows for calculating probable errors more nearly in the usual way. The probable errors of differences were determined throughout by the usual formula, $E_D = \sqrt{E_1^2 + E_2^2}$, in which E_D is probable error of difference and E_1 and E_2 refer to the probable errors of the respective values between which the differences were drawn.

Size of litter.- The second, third, and fourth litters of dams were most favorable as far as size of litter was concerned. The average size of fifth litters was .22 young smaller than fourth litters, which is over seven times the probable error and therefore significant. First litters were less favorable than fifth litters, the difference being .13 $\pm$ .026 young. There were generally small decreases in the litter size with successive litters after the fifth which singly are not statictically significant but taken together indicate a decline. Further, the

frequency distributions for litter size showed that as parity advanced beyond the sixth litter there was a marked falling off in the larger sized litters. Litters of five and six made up 7 per cent of all the young born in second and third parities, 9 per cent of the litters in fourth parities, 5 per cent in fifth parities, 4 per cent in sixth and seventh parities, 1 per cent in eighth parities, 2 per cent in ninth parities, and only one litter of 5 and one of 6 were born in the tenth parities. No litters larger than four were born in the eleventh and twelfth and none larger than three in the thirteenth, fourteenth, fifteenth, and sixteenth parities. Of the 19 litters of 7 born in the stock, 7 were second litters, 7 third litters, 4 fourth litters, and 1 was an eighth litter. Of the 3 litters of 8, 2 were second litters and the other was a third litter. Thus the litter distribution brings out a further advantage for second, third, and fourth litters, which was of course reflected in the average size of litter.

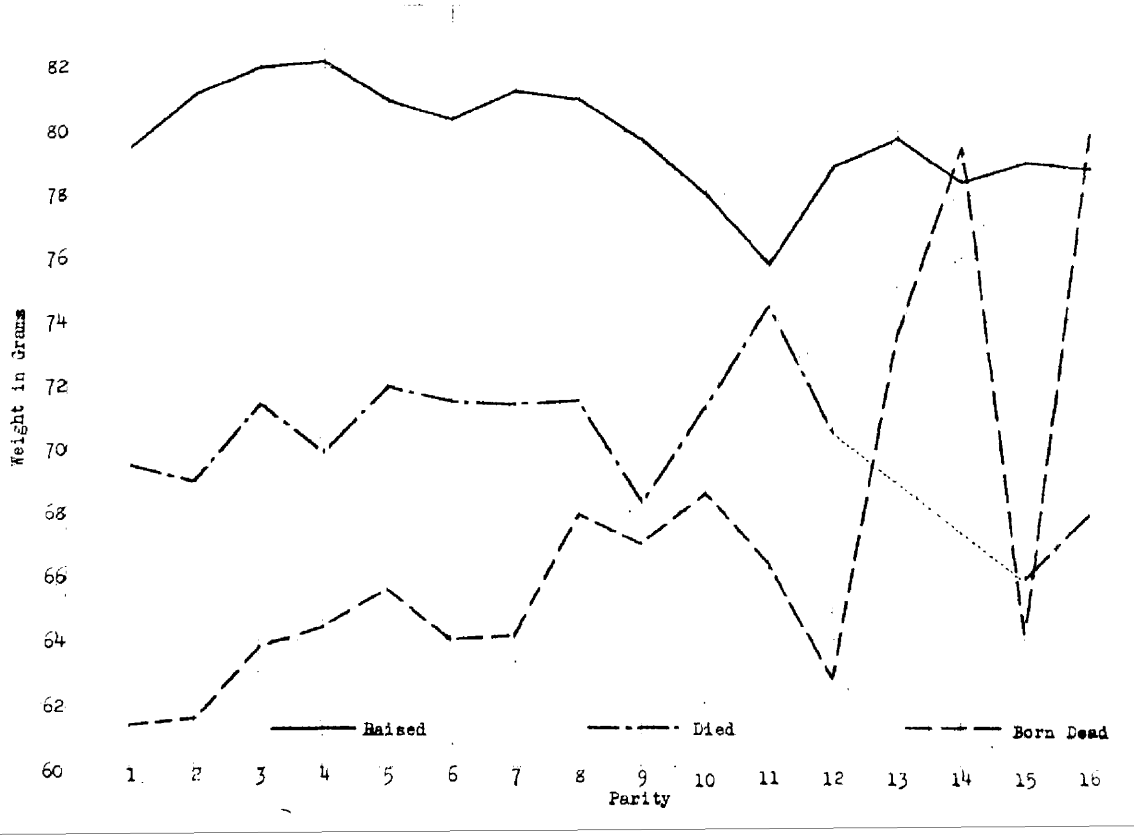
Fate.- The third litters of dams were most favorable for the per cent born alive but the differences between third and fourth litters were not significant. Third litters were more favorable than second litters, and second litters were more favorable than first litters, the differences being 1.86 and 1.85 respectively. Each of these differences are more than four times the probable error. The per cent born alive in fifth litters is 2.22 per cent less than in fourth litters, and in sixth litters it is 3.17 per cent less than in fifth litters. These differences being nearly four times the probable error are probably significant. In succeeding litters there appeared to be a general decline,

Chart XXI

Effect of Parity on Fate and Size of Litter

Chart XXII

Effect of Parity on Birth Weights



though somewhat irregular, and the smaller numbers resulting in larger probable errors tend to make the differences between successive litters of no statistical importance except for the difference between tenth and eleventh litters which seemingly can not be directly concerned with parity.

The comparison of successive litters for percentage raised of born alive showed that about 2 per cent less of young born alive were raised in first litters than in second and third litters, which were the most favorable for this index. Fourth litters were less favorable than third litters, the difference being nearly three times the probable error. There was a difference of 4 per cent between fourth and fifth litters which was 5.4 times the probable error, therefore indicating a significant drop in the per cent raised. In litters after the fifth there appeared to be some decrease but it was irregular, and the differences between successive litters were not statistically significant.

Weights.- The birth weights of the young having different fates show some differences in the relative advantage of different parities. Birth weights of those born dead and died are, however, of no importance for the continuance of the stock, nor would they be of any practical value in the production of our domestic animals. The convergence, however, of the weights of young born dead, died before weaning and raised as parity increases suggests that accidental factors become of more importance in advanced parities. Still births and death before weaning in early litters indicate a long continued condition reflected in low weight of young but in later litters it is a much less indicator since the weights tend to converge.

The birth weights of those which were raised to weaning were largest in the fourth parity, but the difference between the third and

fourth parities is only a little greater than its probable error. Second and fifth litters are at a disadvantage as compared with those born in the third and fourth litters, their differences being 3.9 and 4.2, respectively, times their probable errors. First litters are likewise at a disadvantage as compared with second litters. The differences between successive litters after the fifth parity are not individually significant, but there is a general though somewhat irregular decline.

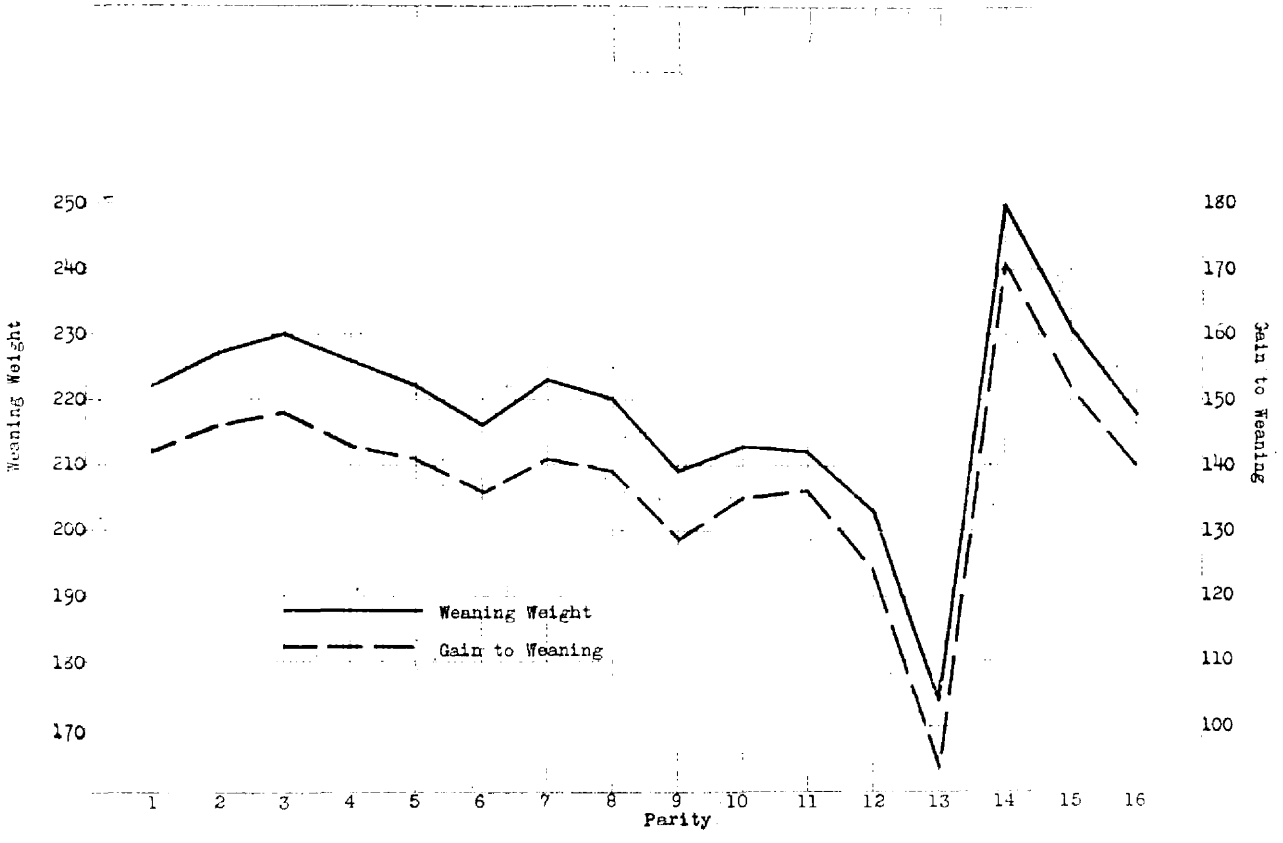
In weaning weights third litters showed advantages of 2.46 ± .714 gm over second litters and 3.90 ± .801 gm. over fourth litters. The average weight of the young at weaning born in first litters was 5.17 ± .685 gm. smaller than in second litters. Young born in fourth, fifth, and sixth parities showed successive decreases in weaning weights as compared with the preceding litters. The reasons why the seventh and eighth litters should be heavier at weaning than sixth litters are not apparent.

The largest gains between birth and weaning were also made by young born in the third parities. The differences in gains of young born in second and third parities was 1.70 ± .611. First litters were at a disadvantage as were fourth and succeeding litters. The advantage of seventh over sixth litters, both in weaning weight and gain to weaning, is quite obviously due to the abnormally low weaning weights of sixth litters which were a result of the very low gains. It is quite evident that the general course is toward a decline after the third litter in weaning weight and gain.

Sex ratio.- The sex ratios showed considerable irregularity but the differences were not significant even in the extremes, 53 per cent males and 38 per cent males, because they occurred in advanced litters

Chart XXIII

Effect of Parity on Weaning Weight and Gain to Weaning



where the numbers were small. No general course seems to be indicated as with most of the other indices.

Analysis of decline.- The decline between the fourth and tenth parities was measured by calculating the regression formula for each of the indices using Fisher's (1928) t value (the relation between the regression and its standard error) as an estimate of the significance of the decline. The values of the constants in the regression equation $Y = \bar{y} + b\ (x-\bar{x})$ are given in Table 26 together with the probable error and the value of t and the probability, P. In this formula x represents any particular parity, $\bar{x}$ the mean of the parities 4 to 10 i. e. 7. Y is the calculated size of litter, weight, mortality, etc., for the particular parity x, $\bar{y}$ is the mean observed value of the index and b is the regression for each deviation in the parity from the mean. The probability, P, was determined from tables prepared for this purpose.

The regression for birth weights of died, weaning weights, and gains cannot be considered as significant. On the other hand size of litter, birth weights of raised, per cent born alive and per cent raised show significant declines which would not be expected to occur in data not showing a decline more than 1 in from over 100 times to 1 in 25 times. Birth weights of born dead show a significant increase with succeeding parities bearing out the reference to the convergence of birth weights of those having different fates which was mentioned above.

It is clear that first litters are produced at a disadvantage in all the characters studied. This is not particularly unexpected when one recalls that the practice in the stock is to make matings at weaning, and conception may occur any time after 33 days of age, and in a few

Table 26

Constants for Regression of Various Indices on Parity.
(Fourth to tenth litters)

Index	a	b	Standard Error	t	P
Size of litter	2.4443	-.06536	.0138	4.736	.0052
Per cent born alive	80.8142	-.7779	.2897	2.685	.043
Per cent raised of born alive	78.2086	-1.1075	.3592	3.083	.027
Birth weights of born dead	65.9314	+.6835	.2390	2.860	.035
Birth weights of died	70.8186	-.1035	.2580	.401	.71
Birth weights of raised	80.5271	-.5271	.1494	3.528	.017
Weaning weight	218.4857	-2.100	1.216	1.73	.14
Gain to weaning	137.9571	-1.589	1.006	1.58	.17

cases the records showed that matings occurred before this age was reached. The dams at the time such litters were born had not reached maturity in growth or development. The prime period for reproduction occurred when second, third, and fourth litters were born. After the fourth litter there followed a general decline in succeeding litters in most of the characters studied. The study did not take account of the effect of changes in the proportion of the families represented in advanced parities resulting from possible differences in the length of life of particular families. A spurious effect of parity might have been brought about in this way, but the decline would hardly have behaved as it did had parity been entirely independent.

Discussion.- Effects of the age of parents on various characteristics have been pointed out in numerous publications but few are based on as large a body of data which has been as accurately recorded as the basic data for this study. Minot (1912) pointed out that the size of litter in guinea pigs increased with age during the first 16 months, which is somewhat more advanced than the present study indicates in which second, third and fourth litters are the most favorable for size of litter. Hammond (1914) Jones and Rouse (1920), and Bartram (1926) reported that the size of litter in the domestic animals increased with age. In humans Jenkins (1927) pointed out that the frequency of multiple births increased with the age of the mother up to 35 to 40 years, after which it fell off rapidly but monozygotic twinning was not affected by age. In the rodents Feldman (1925) reported increases in litter size in the rat with the age of the dam up to 150 to 179 days and King (1924) found that second litters were larger than first litters but after the second there was a gradual decrease in size in subsequent litters. In mice Parkes (1924) found second litters to be largest while

MacDowell and Lord (1924 and 1925) report increases in the corpora lutea counts up to the fifth and sixth litters. Parity was considered of more importance than age. The findings in the rat and mouse agree well with the guinea pig in showing an increase in litter size up to the second, third or fourth litters. They make little comment upon the subsequent decrease in litter size.

In size and growth rate and mature weights there appears to be little relation to parity as was observed in the gains and weaning weights. Prawochenski and Kaczkowski (1926) found the mature weights of sheep little effected tho birth weights and initial growth after birth was better in lambs from mature ewes. MacDowell (1914) and Punnett and Baily (1918) found no significant connection between size of litter, age of dam, season of birth and the mature weights of rabbits.

Little information was found on the relation of the age of the dam or parity to mortality tho much is available on the quality of the offspring, but such runs into an unlimited amount of information having a bearing on the general problem of the inheritance of acquired characters.

Fluctuations in the sex ratio which have been correlated with parity have been reported quite frequently. For example, King (1924) with reference to the rat states "it (sex ratio) is below the norm in early litter cast, rises slowly to a maximum and drops abruptly to a very low point in litters cast at the end of the series." Parkes (1924 II) found decreased percentages of boys associated with advancing age and successive births of the mother; there being 163.8 males per 100 females amongst the children of mothers 13 to 17 years of age and 84.6 males per 100 females amongst the children of mothers 43 years of age. However, Fetscher (1924) found that the percentage of males was increased

in successive pregnancies and with the age of the mother. Sex ratio showed no definite association with parity in the guinea pig.

Summary

From a study of the fertility, birth and weaning weights and sex ratio in an inbred guinea pig colony comprising more than 30,000 individuals born over a period of 18 years the following results were obtained:

1. Size of litter affects birth weights, weaning weights and gains to weaning; the weights being larger in all cases for those born in smaller litters. The reciprocals of the weights were fitted closely by a second order parabola.

2. Size of litter affects the percentages born alive and percentages raised of those born alive; litters of two and three being most favorable but showing that mortality was considerably heavier in larger litters.

3. Size of litter did not affect the sex ratio of the total young born.

4. The birth weights of those which were raised to weaning age were significantly heavier (about 10 grams) than for those which died between birth and weaning, and the birth weights of those born dead were approximately 4.5 grams lighter than those dying between birth and weaning. These differences were maintained quite constantly thruout the different sized litters.

5. Sex was a small but constant factor in influencing birth weights, weaning weights and gains; males being heavier than females in all litter sizes. The birth weights were similarly affected for

those which died between birth and weaning and those raised to weaning, but the difference in those born dead was not significant.

6. The per cent born alive was not affected by sex but over 1% more males than females were raised to weaning of those born alive. This relation was quite uniform in all litter sizes.

7. Correction factors for eliminating the effect of sex and litter size on the birth weights of those born dead, died and raised, weaning weights and per cent raised and for the effect of size of litter on per cent born alive were established.

8. Monthly indices were calculated for 217 months for the frequency of litter, size of litter, birth weights, gains to weaning, per cent born alive, per cent raised of born alive, number of young raised per 100 matings and sex ratio after making suitable corrections for the effect of size of litter and sex of young.

9. Most of the characteristics show quite definite seasonal cycles, conditions being generally unfavorable in the late fall and winter and favorable in the spring and summer. Birth weights show a bimodal seasonal cycle with higher birth weights in the late spring and fall. There were other exceptions in individual characteristics and for particular years. The sex ratio also showed some seasonal variation.

10. From the simple correlations of each of these characteristics with each other over a nine months period it was apparent that

(a) Frequency of litter showed the lowest correlation with itself and with each of the other factors, followed in order by size of litter, indicating variations associated with more immediate conditions. This is also true of per cent born alive to a less extent. On the other hand birth weights, gains and per cent raised of born alive appear to result

from influences operating over a longer time.

(b) Tho the different indices are probably affected by different influences, for simplification of explanation the approximate time in the life history of the animal before which the indices are most likely to be affected has been calculated from the composite relations as 12 days before conception for size of litter, conception for frequency of litter, 24th day of gestation for per cent born alive, 31st day of gestation for birth weights, 37th day of gestation for per cent raised of born alive, and 50th day of gestation for gain. It was estimated that the reaction to an exceptional condition would be expected to manifest itself in birth weight about 37 days later, per cent born alive 44 days, gains 51 days, per cent raised of born alive 64 days, frequency of litter 68 days and size of litter 80 days after the exceptional condition occurred.

11. From the correlations a small but regular negative association appears between the per cent of males and all the other factors indicating favorable conditions. There appears to be a heavier prenatal mortality of females when other conditions are unfavorable or a lesser prenatal mortality of males when other conditions are favorable.

12. Most of the indices except sex ratio showed a significant relation to parity; first litters were less favorable than second litters for size of litter, per cent born alive, per cent raised, birth weights of born dead and raised, weaning weights and gains. The birth weights of those dying between birth and weaning remained constant in all parities, while birth weights of born dead showed a constant rise with advanced parities. All other indices except weaning weight and gain showed a

significant drop from the fourth to the tenth parities. The most favorable parities were as follows: size of litter, second, third and fourth; per cent born alive, third and fourth; per cent raised, second and third; birth weights of raised, third and fourth; and weaning weights and gains third.

PART II

INTRAUTERINE FERTILITY

The various phenomena associated with the development of the graafian follicle and its maturation, fertilization by a sperm cell, normal development of the zygote, implantation, fetal nutrition, parturition, and preparation for nourishing the young after birth are physiologically very complex. Little progress has been made on the study of the maturation of the follicle further than to point out that such is associated with the occurrence of the heat period in the various classes of animals. It has been shown that there is heavy elimination of follicles at various stages. Marshall (1922) states that the human ovary at puberty contains 20,000 oocytes. Arai (1920) estimated that there were 35,100 ova in the ovaries of rats at birth, but these were reduced to 11,000 after 23 days and 6,000 by 63 days after birth. Allen, Kountz, and Francis (1925) found 41 developing follicles in the sow 10 days after oestrum, 22 to 23 at 12 days, and 17 at 15 days after oestrum. Robinson (1918) believed that the smaller follicles were necessary for providing nourishment for the larger developing ova in the ferret, and Loeb (1917) prevented maturation of the follicles in the guinea pig and caused them to atrophy before reaching medium size by pronounced undernourishment. It is thus apparent that competition or selection

of animals is not limited to the time after birth, but before the zygote is formed such a process is underway amongst the female gametes as well as the male gametes; it being commonly recognized that many more sperm are produced than can be utilized for fertilizing the ova that mature. It also seems certain that environmental conditions may influence the amount of elimination.

After the maturation of the follicles, the liberation of the ova and their fertilization by the male gamete, the selective elimination continues among the zygotes during the period of intrauterine life for which such extensive preparation in the uterus for the implantation and the nourishment of the foetus has been made. There has been much work reported on the oestrus cycle of the various classes of animals, which was referred to in Part I, but most of it has been primarily concerned with the duration of the periods and means of identifying the heat period with accuracy and in the living animal. Loeb has no doubt contributed more on the particular action of the various organs and glands and the influence of their secretions on the reproductive processes in the female with especial reference to the guinea pig than any other investigator. Several of his more recent papers, which summarize his findings, are cited. Slightly different interpretations as to the functions of particular organs were given by Papanicolaou (1923), Stockard (1923) and Corner (1928).

The importance of prenatal mortality as a component of the fertility of animals is well recognized and estimates are now available on the normal amount in most of the common domestic and experimental animals.

The study here reported was concerned with fertility and prenatal mortality or more specifically differences between the number of ova produced as determined by the number of corpora lutea in each ovary and the number of normal foetuses found in the uterus of pregnant females in different families and in different matings.

Materials and Methods.

For this portion of the work five large pens about four feet square were selected, and mature males from the five inbred families which had been produced after 20 to 25 generations of brother and sister matings were put in the different pens. These pens, which were located in the guinea pig house of the Division of Animal Husbandry of the United States Department of Agriculture, at Beltsville, Maryland, were designated as 2, 13, 32, 35 and 39, corresponding to the number of the inbred family from which the males in the particular pen were derived. As females from the same inbred families or from the control or crossbred stocks were weaned and were not needed for other experiments they were placed in the different male pens, being careful to get an approximately equal distribution of the females from a particular family in each pen.

The females were examined at weekly intervals and killed at as close to parturition as one could estimate. Prior to killing a female her live weight was determined, as well as her number, age, and a record of her family, generation, birth weight, and weight at weaning.

After killing the females a careful post mortem examination was made. Each ovary was then examined macroscopically for corpora lutea

by sectioning with a scalpel. It seemed rather difficult to determine the presence of corpora lutea with certainty at the advanced stage of gestation by examining the surface of the ovary, but by sectioning the ovary the large corpora lutea stood out very clearly from the ovarian stroma. Following the record of the corpus luteum count for each ovary the distance between the centers of the placentae and the free space in the uterus between two placentae were measured and recorded as accurately as possible. An indication was also made in this connection of the relative position of implantation in regard to the attachment of the broad ligament about which implantation always takes place. An estimate of the blood supply was also made at the same time. Confidence in the accuracy of the measurements and descriptions of these conditions was, however, not sufficient to warrant their use in the analysis of the data.

The uterus was next opened, beginning at the vagina and cutting up thru each cornu, always cutting on the ventral surface in order not to injure the attachments and cause confusion as to the location of each foetus where there were several. The membranes of the individual foetuses were examined for the presence of clotted blood and the placentae were likewise examined. Frequently hemorrhages occurred between the decidua and the placentae and the presence of more or less blood in different stages of decomposition and absorption was frequently observed. Each foetus was removed from the membranes and its position, sex, weight, crown-rump length and left foot length recorded. Each placenta was also weighed and the diameter in two perpendicular directions measured. There was some loss of blood upon severing the

umbilical cord but by delaying somewhat after a female was killed before making the records on the embryos this was reduced to a minimum.

A total of 352 females were killed as described within about 15 months and the data recorded on the embryos. There was considerable variation in the age of the dams at the time they were killed. This was partly due to the fact that some females were missed, or the stage of gestation was underestimated and the first litters were born, which made it necessary to wait for another gestation period; others aborted and in some cases individuals appeared to have aborted several times in succession. No reliable records were obtained in this respect, however, because of the number of females in a particular pen and the probability of overlooking most of the abortions. The larger differences of the age of the females when killed, however, appeared to be due to differences in the breeding age of the females. This was evidently a matter of development and early growth. Those females which were poorly developed also seemed to be slow in maturing sexually. There was also a relation to the family from which the male was taken. The females in ♂ 13 pen were particularly slow at breeding while those in ♂ pen 39 were bred relatively young. More males were placed in ♂ 13 pen as soon as the condition became apparent, but this had no noticeable effect in reducing the age of conception.

The stage of gestation which the females had reached at the time they were selected for study varied somewhat. This was particularly

true in the beginning, as some experience was necessary before the intrauterine age of the embryos could be estimated with any degree of accuracy. Prior to undertaking this work the embryos of nearly 300 females which died in different stages of gestation were examined and attempts made to estimate the gestation period. Measurements and records were kept on such embryos in much the same way as for those studied in the experimental breeding work. Such characteristics as the size of the head and the amounts of embryonic fluids that appeared to be protecting the head as determined by palpation were of most value in estimating the stage of gestation. The relative size of the female and the expansion of the abdomen were too deceptive to be of any value, as females with small litters would reach parturition without any noticeable expansion of the abdomen, while those with large litters would show greatly distended abdomens long before parturition. It was, therefore, a matter of carefully examining each one at weekly intervals. There is, of course, a possibility that the frequent handling and examination may have had an influence on the prenatal mortality but this seems very doubtful as the greatest of care was exercised in handling the females in order that the developing embryos be uninjured.

Notwithstanding the care taken in making the estimates of the stage of gestation, there was some tendency to kill the females with larger litters earlier in the gestation period than females with fewer embryos. The extremely large abdomen of such females naturally called attention to them, and the fact that it frequently seemed impossible for the dam to become any larger influenced judgment on these, so that

rather than risk losing a litter such females were frequently killed earlier in the gestation period than was really desirable.

The ages of the foetuses after killing the dams were estimated in 5 day intervals according to their size, the condition and pigmentation of skin and development of the hair, nails, etc. The estimates were based on observation of the young in over 300 uteruses from pregnant females which died in the stock, many of which had had previous litters, and the time of conception could be reckoned from that time, and from a few timed embryos in which cases the date of conception was known by removing the female from association with a male on the day following parturition, so that conception, if it occurred at all, must have occurred on that date.

Among the 352 pregnant females killed for study there were 14 in which the number of foetuses exceeded the numbers of corpora lutea. As these records would materially affect the percentages of ova missing and prenatal mortality based on corpus luteum counts, the result with this group of irregular females is not included in the calculations for the different families, but is discussed separately. There were, therefore, 338 females considered in the regular litters. Of these there were 8 females the sires of whose litters were unknown. These were averaged in with the females for particular families, but obviously had to be considered separately in the tabulations of the litters produced by certain sires.

Distribution of females by families.- Table I shows the distribution of the 338 females according to the number of females from each of the families that were mated in each of the male pens.

In this connection the description of the breeding of the families is of interest. ♂ 2, ♂ 13, ♂ 32, ♂ 35 and ♂ 39 refer to pens

in which males from the respective inbred families described by Wright (1922) were placed. ♀ 2, ♀ 13, ♀ 32, and ♀ 35 refer to females from the same families. No females were available from family 39 for this experiment. Difficulties experienced in keeping this line going made it necessary to use all the available females for that purpose. ♀ Inbreds refers to a combination of all the females from the inbred lines. ♀ B refers to the control stock in which no matings closer than second cousins were made. ♀ CY-O are from the cross of inbred families 2 and 13 which were made for the purpose of developing a strain producing a large percentage of cyclopeans. ♀ CY-1 and ♀ CY-2 are the first and second generation inbred offspring from CY-O. Total CY♀s are the totals for the groups ♀ CY-O, ♀ CY-1 and ♀ CY-2.

The symbols < and > 120 days indicate those for which the age at conception was less than and greater than 120 days, respectively. This age was taken as an empirical division point to separate the dams according to age at conception. Age at time of conception was, of course, determined as the difference between the estimate of the gestation period of the young at the time the dam was killed and the age of the dam at that time.

It is quite evident from the table that the small numbers of females from family 35 mated in the different male pens make any comparisons of this family with others of practically no value. There were a total of only 9 females from this family in the experiment. Further than this the small numbers of females from any of the families mated in a particular male pen make comparisons of little value. Therefore, in most cases emphasis has rather been placed on the total females from

TABLE I.

NUMBERS OF DIFFERENT TYPES OF MATINGS

Family of females	Male Pens															Total females[1] from each family		
	♂ 2			♂ 13			♂ 32			♂ 35			♂ 39					
	Age at conception		Total	Age at conception		Total	Age at conception		Total	Age at conception		Total	Age at conception		Total	Age at conception		Total
	<120 days	>120 days		<120 days	>120 days		<120 days	>120 days		<120 days	>120 days		<120 days	>120 days		<120 days	>120 days	
♀ 2	13	2	15	7	5	12	5	8	13	2	5	7	12	2	14	40	22	62
♀ 13	13	1	14	10	1	11	8	4	12	5	2	7	6	4	10	43	12	55
♀ 32	8	0	8	7	2	9	6	3	9	8	2	10	11	0	11	41	7	48
♀ 35	1	0	1	0	1	1	2	1	3	0	1	1	0	2	2	3	6	9
♀ Inbreds	35	3	38	24	9	33	21	16	37	15	10	25	29	8	37	127	47	174
♀ B	12	1	13	7	3	10	11	2	13	9	2	11	9	3	12	51	11	62
♀CY-0	4	0	4	3	3	6	6	0	6	4	0	4	4	0	4	21	3	24
♀CY-1	9	3	12	6	5	11	7	4	11	9	1	10	7	3	10	39	16	55
♀CY-2	5	1	6	2	2	4	4	2	6	2	1	3	4	0	4	17	6	23
Total CY ♀s	18	4	22	11	10	21	17	6	23	15	2	17	15	3	18	77	25	102
Total ♀s	65	8	73	42	22	64	49	24	73	39	14	53	53	14	67	255	83	338

[1] Includes 8 females for which sires of the litters were unknown.

the particular family mated in all the male pens or the total females from all families in a particular male pen.

It is difficult to understand how the family from which a male is derived could have any effect on the number of corpora lutea which a female produces except in an indirect way. For instance, if males of a particular family were slow breeders and the females were more mature the number of ova produced would be expected to be larger, according to the data reported in Part I. This is, of course, truly a result of the age of the dam at conception.

Results.

In preliminary efforts to analyze the differences in number of ova produced by females from different families and a study of the comparative prenatal mortality, a factor which appeared to be complicating the situation was the age of the dam at the time of conception. For this reason the variation in the age of the females will be discussed first.

Age of females at conception.- It was observed early in the experiment that females were being removed at an earlier age from certain of the male pens than from others. Efforts were, therefore, made to lower the age of breeding in the slower breeding pens by the addition of more males, but this seemed to be without avail. Male pens 39 and 2 were particularly rapid breeders, while females remained in male pen 13 a long time before breeding, thus making the age at which the females were to produce litters much more advanced.

Casual observation also indicated that the males were by no means entirely responsible for the age of breeding, as females from certain

families, particularly B, were regularly younger than the females from the other families when pregnancy was detected.

The average age at conception of the females of the different families mated with males from the different families is given in Table 2. For the 338 females the average age at conception was 97.02 days while the 255 females for which conception was estimated at less than 120 days averaged 71.52 days and the 83 females which were over 120 days at conception averaged 175.36 days of age when conception occurred. There was thus considerable variation in the age at conception.

It is felt that the group conceiving under 120 days is the most comparable for the purposes of study as certain of those in which conception occurred after 120 days were no doubt second litters, as a few such females were observed to be pregnant and so recorded, whereas a week or two later they were not pregnant. Particular individuals were probably shy breeders or for some reason did not become pregnant until advanced age, which in two cases ran over 350 days. It is thus quite apparent that the group under 120 days served as the most uniform comparison of normal females by eliminating exceptionally slow breeders which with the small numbers involved had a very pronounced effect on the average. This is very clearly brought out in Chart XXIV, showing the average age at conception for all females in the different male pens as compared with females conceiving at less than 120 days of age. There were but 6 CY-O females mated with family 13 males and the average age at conception for the three conceiving under 120 days was 72 days and for the 3 over 120 days was 135 days, but 1 was over 300 days.

TABLE 2.

AVERAGE AGE OF FEMALES IN DIFFERENT MALE PENS AT CONCEPTION.

Family of females	Male Pens ♂ 2			♂ 13			♂ 32			♂ 35			♂ 39			Total[1] females from each family		
	Age at conception <120 days	Age at conception >120 days	Total	Age at conception <120 days	Age at conception >120 days	Total	Age at conception <120 days	Age at conception >120 days	Total	Age at conception <120 days	Age at conception >120 days	Total	Age at conception <120 days	Age at conception >120 days	Total	Age at conception <120 days	Age at conception >120 days	Total
♀ 2	86	197	101	80	229	142	83	172	138	106	166	149	80	170	92	84	186	120
♀ 13	65	133	70	83	255	99	73	152	99	78	154	99	78	131	102	74	154	91
♀ 32	78	---	78	71	142	86	69	203	114	67	150	84	71	---	71	71	170	85
♀ 35	102	---	102	--	201	201	59	180	99	--	178	178	--	162	162	73	176	142
♀ In-breds	77	176	85	78	209	114	73	173	116	76	162	110	76	152	92	76	174	102
♀ B	65	208	76	68	183	102	59	126	69	63	134	76	64	141	83	62	155	79
♀ CY-0	64	--	64	72	235	154	68	--	68	76	--	76	55	--	55	67	235	88
♀ CY-1	61	176	90	77	206	136	76	167	109	70	157	79	83	148	102	72	177	102
♀ CY-2	71	131	81	101	174	137	59	220	113	52	224	109	78	--	78	71	190	102
Total ♀ CY s	64	165	83	80	208	141	69	185	99	69	191	83	74	148	86	70	187	99
Total ♀ s	71	174	82	77	205	121	68	172	103	70	162	94	74	148	89	72	175	97

[1] Includes 8 females for which the sires of the litters were unknown

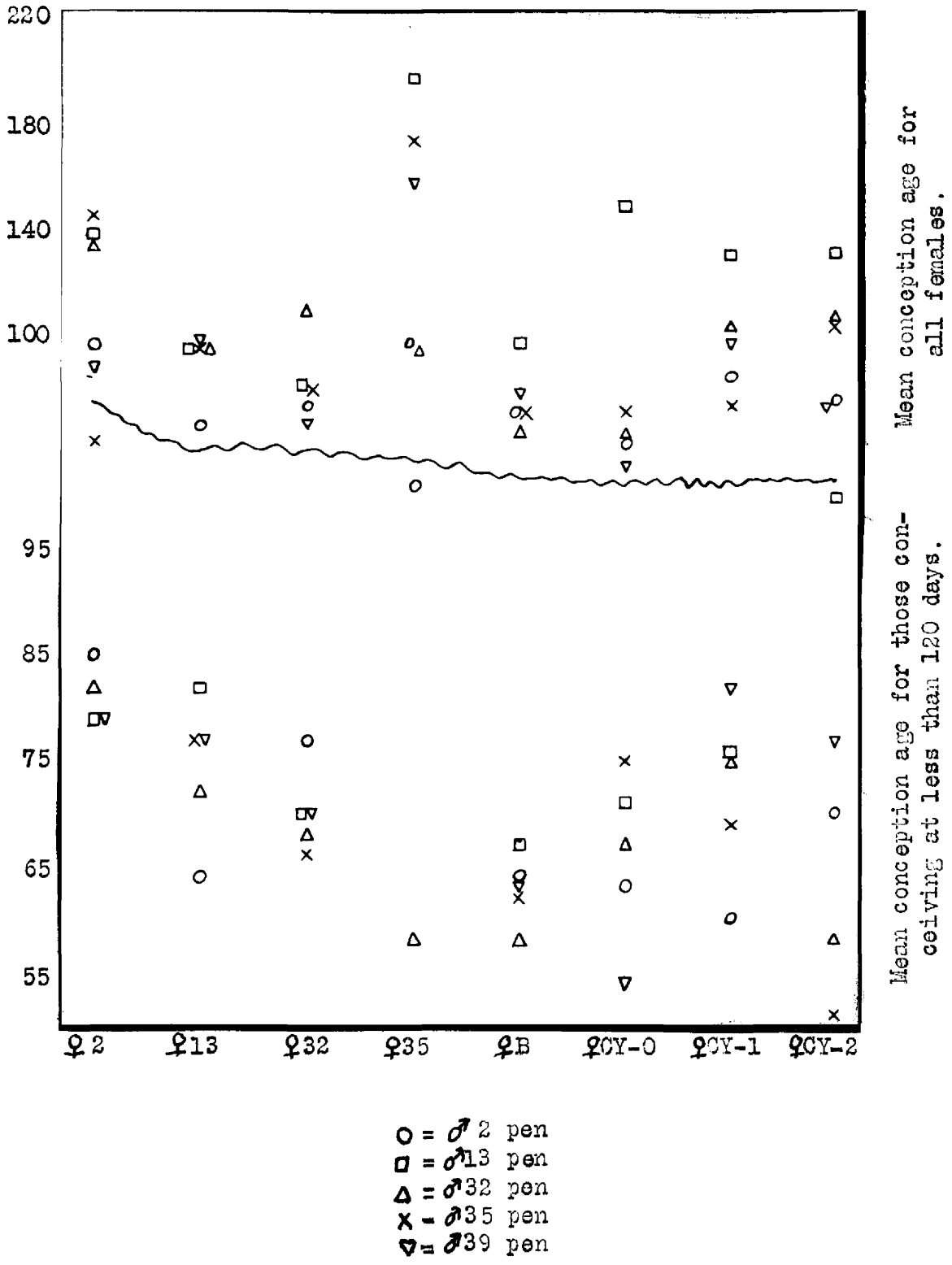
Thus the average conception age is much advanced for the females in the latter group as compared with the other groups but in those less than 120 days the average age at conception is quite comparable to the age of the CY-O females in the other male pens at conception.

This chart serves as a basis for comparing the rate of sexual maturity of the different families. It is interesting to note that there is considerable variation in the average age of breeding of females from family 2, but they are mostly all older than females from the other families. Females from family 13 breed somewhat younger (average 91 days) and females 32 still younger, the average age being 85 days. It is also of interest that in the < 120 day group the age at conception of family 32 females was very uniform in all male pens. The comparatively vigorous B stock bred at the youngest average age which was 79 days. The order of the age of the females from the different families, i. e. ♀ 2 oldest, ♀13, ♀ 32, and ♀ B youngest was closely approximated in the male pens notwithstanding considerable variation in the average ages in these pens. In the >120 day group ♂ 32 pen, ♀ 32 were older than ♀ 13 or ♀ 2, while the age of breeding of ♀13 was slightly younger than ♀ 32 and ♀ B for all females in ♂ 2 pen. CY-O females bred at an average age of 88 days, very similar to the age of breeding for females from family 13. In the CY-1 and CY-2 females there was greater variability in conception age for those breeding under 120 days, but this is not brought out for all females.

It is curious that if the matings of the CY females in the male 13 pen be eliminated, the slow breeding of the males from family 13 is not so pronounced, though the age at breeding of females from all

Chart XXIV

Age of females in different male pens at conception.



families was relatively advanced when mated in male 13 pen. On the other hand, the CY females in all the other male pens conceived at a younger age than the inbred females in those pens.

The possibility of a greater likelihood of males mating with females from the same or conversely from different or particular families at younger ages occurred but the data do not clearly show any other indication of such. Both Feldman (1925) and Macomber (1923) called attention to such conditions causing sterility in the rat, certain matings proving sterile though both individuals proved fertile in other matings. Families 2, 13 and 32 are the only ones from which sufficient females were available for a comparison of this kind.

Number of corpora lutea per pregnancy.- The females from the different families showed considerable variation in the numbers of corpora lutea produced. Such was also apparent for females from the same families in different male pens and for all the females in particular male pens. Further than this there were considerable differences between the average numbers of corpora lutea produced in the 2 ovaries. These differences do not prove to be significant when treated statistically, except in a few possible cases in regard to the right and left ovary, but frequently in other groups of females from the same families the balance is thrown in favor of the opposite ovary.

Table 3 gives the average number of corpora lutea found in the left and right ovaries of the females from the different families mated in each male pen. The small numbers of females from each family in the different pens make the differences of no statistical significance, but the totals for all females of family 2 and family 32 taken together

TABLE (3)

AVERAGE CORPORA LUTEA COUNTS PER LITTER IN LEFT AND RIGHT OVARIES

Females of All Ages

Family of females	Male pens										Total females from each family[1]	
	♂2		♂13		♂32		♂35		♂39			
	Left ovary	Right ovary	Left ovary	Right ovary	Left ovary	Right ovary	Left ovary	Right ovary	Left ovary	Right ovary	Left ovary	Right ovary
♀ 2	1.33	1.20	1.33	1.25	1.46	1.31	1.86	1.00	1.64	1.00	1.50	1.16
♀13	1.07	1.50	1.45	1.18	1.33	2.00	1.86	1.57	2.10	.90	1.49	1.44
♀32	.75	1.13	.89	1.33	1.11	1.33	1.20	1.20	.82	1.45	.94	1.29
♀35	1.00	1.00	2.00	1.00	1.00	2.00	2.00	2.00	2.00	1.00	1.44	1.56
Inbreds	1.11	1.29	1.27	1.24	1.30	1.59	1.60	1.28	1.54	1.11	1.34	1.30
♀B	1.15	1.08	1.60	1.30	.92	1.69	1.18	1.18	1.25	1.33	1.21	1.34
♀CY-0	1.00	1.00	1.00	1.17	1.00	.83	2.00	.75	1.25	1.50	1.21	1.04
♀CY-1	1.25	1.25	1.36	1.45	1.64	1.00	1.20	1.20	1.00	1.70	1.29	1.31
♀CY-2	1.00	1.33	1.00	1.50	.67	1.67	2.00	1.67	1.50	1.00	1.13	1.43
♀CYs	1.14	1.23	1.19	1.38	1.22	1.13	1.53	1.18	1.17	1.50	1.24	1.27
Total	1.12	1.23	1.30	1.30	1.21	1.47	1.49	1.23	1.39	1.25	1.28	1.30

[1] Includes 8 females for which the sires of the litters were unknown.

indicate differences in the potential capacity of the left and right ovaries to produce ova. In family 2 females the average number of corpora lutea in the left ovary exceed the number in the right ovary in each of the groups in the different male pens. The average number of corpora lutea in the left ovary was 1.50 ± .088, and in the right ovary 1.16 ± .073, with a difference of .34 ± .114. The females of family 32 show a similar condition except that the right ovary has the larger number in all groups except in male pen 35 where the numbers in the 2 ovaries are the same. There was an average of 1.29 ± .075 corpora lutea in the right ovaries and .94 ± .085 corpora lutea in the left ovaries of all 32 females, the difference in this case being .35 ± .114 ova in the 2 ovaries per litter.

The females from family 13 show as great variation from the left to the right ovary in the different male matings but they are not in the same direction and they are practically equal for all the females from this family. Females of family B likewise reverse in the variations of the corpora lutea counts in the left and right ovaries. None of the CY groups are uniform in indicating a greater production of ova by one ovary than the other.

If the differences in the production of ova by the left and right ovaries of the females of family 2 and 32 are of significance, one would expect considerably less difference between the production of ova in the 2 ovaries by the females from all families mated in each male pen than were observed in these families since no particular family of females predominates in any. When one considers the variation in the counts in the left and right ovaries from the females of all families

killed from each male pen there is almost as much difference between the 2 ovaries. There is a difference in favor of the right ovary for the females from male 32 pen of .26 and in male 35/pen of .26 in favor of the left ovary, which, of course, are less than were shown in the females from families 2 and 13 but they closely approach them in size.

Further than this the distribution of the corpora lutea in the two ovaries grouped according to the female family does not show any regular deficiency in a particular ovary. To be sure there is some irregularity in the distribution for individual families, but there is no pronounced evidence that a particular ovary, either the left or the right, in any family is not functioning normally.

In this connection it is of interest to study the combinations of corpora lutea observed in the females killed. Where 1 corpus luteumis found it may be in the right ovary or in the left ovary. Where 2 are found there are 3 possible combinations, 2 in the left ovary, 2 in the right ovary, or 1 in each ovary. With 3 corpora lutea there are 4 possible combinations, 3 in the left ovary, 3 in the right ovary, 2 in the left ovary and 1 in the right ovary, or 1 in the left ovary and 2 in the right ovary, etc. The frequency of each possible combination is given in Table 4. In this table the number of corpora lutea are given which corresponds to the primary size of litter. In the column headed distribution of corpora lutea L stands for left ovary and R for right ovary. Thus LORI designates pregnancies in which there were no corpora lutea in the left ovary and one in the right ovary. The distributions are given for females from each family as well as the total inbreds, total CYs and all females combined.

TABLE 4.

DISTRIBUTION OF THE CORPORA LUTEA IN THE 2 OVARIES ACCORDING TO TOTAL NUMBER OF CORPORA LUTEA

Females of all ages

Number of Corpora Lutea	Distribution of Corpora Lutea	Number of females from each family										
		2	13	32	35	B	CY-0	CY-1	CY-2	Inbreds	CYs	Total
1	(L0R1	1		5		3	1		1	6	2	11
	(L1R0	1	1				1			2	1	3
2	(L0R2	8	4	11		9	3	7	3	23	13	45
	(L1R1	9	9	13	2	16	10	15	5	33	30	79
	(L2R0	7	6	5	1	6	2	5	4	19	11	36
3	(L0R3	3	2	2		1		4	3	7	7	15
	(L1R2	6	15	4	2	9	1	7	2	27	10	46
	(L2R1	16	5	4	1	9	4	10	1	26	15	50
	(L3R0	4	2	2		1	1	3		8	4	13
4	(L0R4					1			1		1	2
	(L1R3	1	1		1					3		3
	(L2R2	3	2	2	2	4	1	1		9	2	15
	(L3R1		2			2		2	3	2	5	9
	(L4R0	3	1							4		4
5	(L0R5											
	(L1R4											
	(L2R3		2					1		2	1	3
	(L3R2		2			1				2		3
	(L4R1											
	(L5R0											
6	(L0R6											
	(L1R5											
	(L2R4											
	(L3R3											
	(L4R2		1							1		1
	(L5R1											
	(L6R0											

The distribution of the individual families are so variable that it is difficult to make any statements about them, but as the groups are combined, making larger numbers, it is interesting to note that where 2 or 3 corpora lutea are produced the distribution follows close to that to be expected according to random distribution with 3 or 4 combinations of 2 or 3 coins, each of which has an equal chance of falling heads or tails. The 45:79:36 ratio obtained is close to the 1:2:1 ratio to be expected on such a hypothesis. So does the 15:46:50:13 ratio approach 1:3:3:1.

Assuming a distribution of the corpora lutea which appears to be random between the two ovaries, the question is raised if the two ovaries are entirely independent of each other, as concerns the number of corpora lutea which each produces? There is considerable evidence to indicate that the ovaries are under a central control or a limitation acting on both together. For instance, the animals and man ordinarily producing 1 at birth rarely produce dizygotic twins, indicating a capacity for the control of the ability to bring but a single follicle to maturity.

In analyzing the guinea pig data from this standpoint the following constants were calculated for all females, in which the subscripts L, R, and T refer to the corpora lutea in the left and right ovaries and the total number produced per pregnancy:

$\text{Mean}_L = 1.284$ $\text{Mean}_R = 1.302$ $\text{Mean}_T = 2.586$

$\sigma_L = .934$ $\sigma_R = .837$ $\sigma_T = .814$

$CV_L = 72.7 \pm 2.7\%$ [1] $CV_R = 64.3 \pm 2.2\%$ [1] $CV_T = 31.5 \pm 0.9\%$ [1]

$r_{RL} = -.583 \pm .024$

The lack of significant differences between the numbers observed in the left and right ovaries indicates that the ovaries are equal in their capacity to produce ova. The standard deviation of the total being less than the standard deviation in either ovary reduces CV_T to less than half CV_L or CV_R, indicating a more complete control over the total number of ova produced at a pregnancy and less control as to how they will be distributed.

These results are mainly in accord with the hypothesis of Danforth and de Aberle (1928) in which it was considered that three factors regulated or controlled ovulation; (1) the physiological status of the animal as regards age, condition, relation to environment, etc., which control the total number of ova that the animal is able to mature; (2) an influence acting in opposition to the preceding, tending to lessen the correlation between the number produced in the two ovaries; (3) a reciprocal relation between the output of the two ovaries, due to the limitation on the total number of ova produced per pregnancy.

Lipschutz (1927) from studies of ovarian activity after excision of portions of the ovarian tissue, and Lipschutz (1925) and Lipschutz and Voss (1925) conclude that the number of follicles ripening depends on general internal factors rather than on the total number of primary

[1] The probable error of the coefficient of variability was calculated by the formula $.6745 \frac{CV}{2n}\sqrt{1+2\left(\frac{CV}{100}\right)^2}$

follicles present. Hartman (1925) and Asdell (1924) also found extensive hypertrophy of the remainder of the ovarian tissue after removing the greater portion of the ovaries. In the opossum more than the normal number of ova for both sides was produced, while in the rabbit the number of ova was only 10 to 13% less after removal of one ovary and part of the other than was ordinarily produced by both ovaries.

It thus must be concluded that there is a central control over the two ovaries governing the total number of ova produced at a pregnancy, tho the distribution is random with an equal capacity in each ovary.

Effect of age on fertility.- In Part I the size of litter was shown to be related to parity, first and second litters being smaller than third and fourth litters. The data for the age of the dams were not brought into that analysis. It is, therefore, of interest to check up on the effect of age of the females at conception on the number of corpora lutea found in the ovaries. Table 5 gives the mean corpus luteum counts for the females of each family which conceived at less than 120 days as compared with those conceiving at more than 120 days and for all fe males of the particular family. The average ages of these groups which varied considerably in different families are given in Table 2. The results show that the number of corpora lutea produced in each family averages larger for the older groups of families except for the CYO females, but in this case there were only three females in the $>$120 day group. The differences were approximately three times their probable errors in most cases. In further

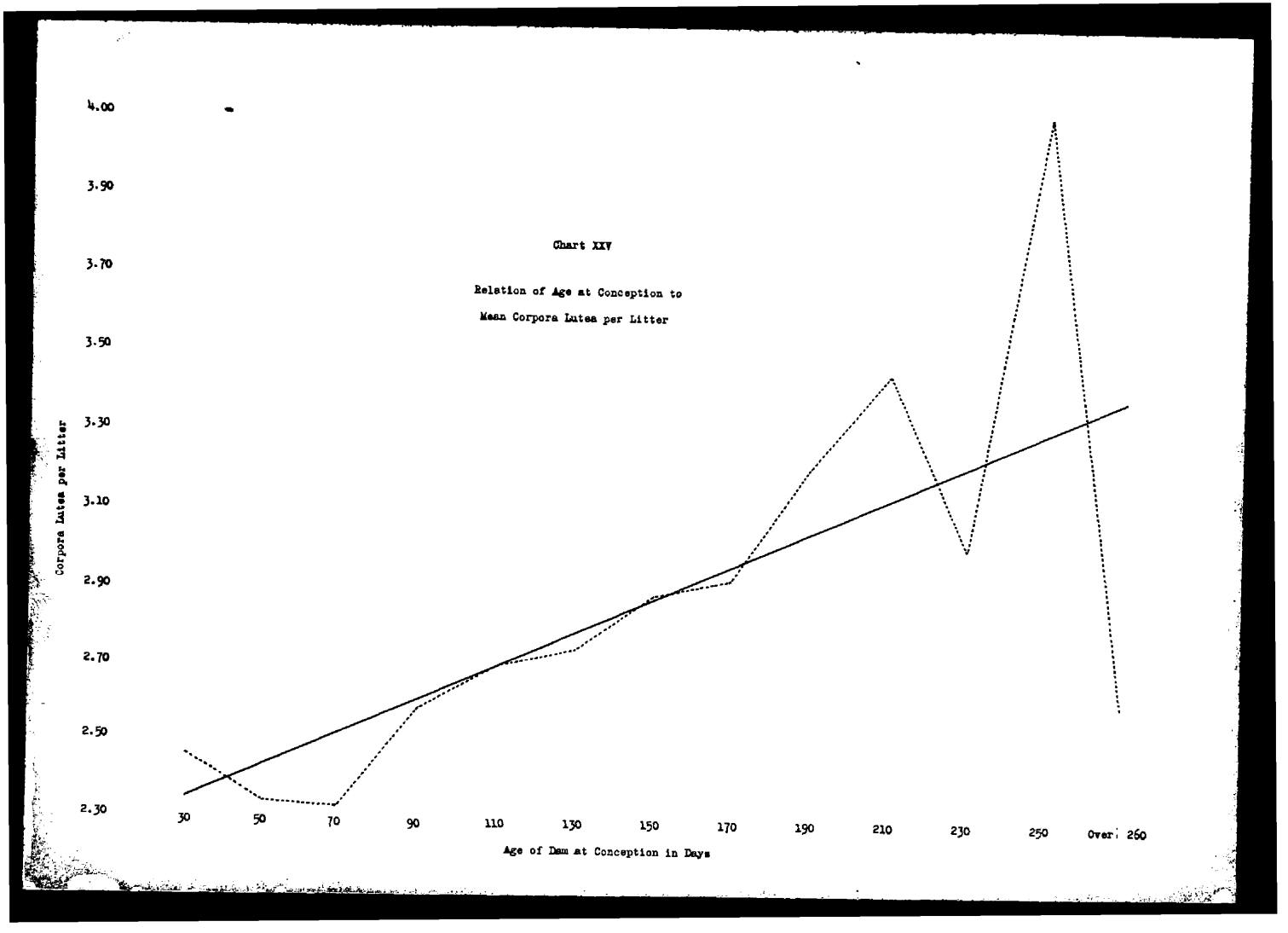


Chart XXV
Relation of Age at Conception to
Mean Corpora Lutea per Litter
Corpora Lutea per Litter
4.00
3.90
3.70
3.50
3.30
3.10
2.90
2.70
2.50
2.30
30
50
70
90
110
130
150
170
190
210
230
250
Over 260
Age of Dam at Conception in Days

testing these differences Fisher's adaptation of Student's method of determining differences t[1] was found to equal 3.2043.

In Fisher's table for t values when there are 6 degrees of freedom there are 2 chances in 100 of the value of t being above 3.143. Thus, there are 49 chances to 1 that the value is significant.

The females from all families were grouped together in 20 day intervals according to the age at conception, and there was found to be a correlation of .341 $\pm$ .032. The average corpus luteum count for the females in each age group are plotted in Chart XXV and show a definite increase with age from those having a mean age of 70 days, in which the average count was 2.32 to 3.44 for those having a mean age of 210 days. The first two age groups are high, probably because such females must have been exceptionally vigorous to conceive at such young ages, and the numbers in the 250, 270 and over 260 age groups were small, these being only 5, 2 and 5 females in the respective groups The regression line fitted to the data shows close agreement except in the extremes. The regression coefficient was +.08654 for each 20 day increase in age and its standard error[2] $\pm$.02590 giving a value for t[3] of 3.341. This is to be expected in a random sample less than once in 100 trials. It must, therefore, be concluded that the age of the dam is

[1] $t = \frac{M\sqrt{n}}{\sigma}$ in which M is mean, n is the number of differences and σ is standard deviation of the differences.

[2] Standard error of regression coefficient equals $\sqrt{\frac{\Sigma y^2 - na^2 - b^2 \Sigma x^2}{(n-2)\Sigma x^2}}$

[3] $t = \frac{b}{s_b}$ in which b is regression coefficient and s_b its standard error.

related to the number of ova produced at an oestrus period and must, therefore, be taken into consideration in a comparison of the corpus luteum counts.

Relation of corpus luteum count to family.- Table 5 gives the average number of corpora lutea produced by the females of each family. These data may be compared with the size of litter as recorded by Wright (1922) for each of the families from 1916-19. In Wright's data the largest litters were produced by B females, the average being 2.65 while in the present data B females produced very close to the smallest litters.

This is probably due to the age of the females at conception. Reference to Table 2 shows that B females in (120 groups averaged 62 days at conception, or 79 days for all pregnancies, which are the youngest for any group. Twenty-six of the B females conceived at less than 60 days and none of these females produced more than 3 corpora lutea, 17 producing only 2. It is thus apparent that the differences in the ages at which the females conceived makes a comparison of the number of corpora lutea inaccurate. Elimination of those conceiving at younger ages does not make a proper comparison as such females, if given an opportunity to mate later, would probably have produced much larger litters than those which, because of lack of development, did not mate until 80 or more days of age.

The inbred females rank in the same order in number of corpora lutea as for the size of litter in Wright's (1922) data, females from family 13 producing the largest litters, followed in order by females of families 2 and 32. In the present data the small numbers of corpora

TABLE 5.

MEAN CORPORA LUTEA COUNTS FOR FEMALES OF DIFFERENT FAMILIES AS AFFECTED BY AGE.

Family	Age at Conception		All Ages
	Less than 120 days	More than 120 days	
	No. of Corpora Lutea	No. of Corpora Lutea	No. of Corpora Lutea
♀ 2	2.550±.071	2.864±.111	2.661±.062
♀ 13	2.698±.088	3.750±.205	2.927±.063
♀ 32	2.171±.070	2.571±.201	2.229±.067
♀Inbreds	2.480±.046	3.085±.091	2.644±.044
♀ B	2.373±.068	3.364±.163	2.548±.071
♀CY-0	2.286±.095	2.000±.389	2.250±.093
♀CY-1	2.462±.074	2.938±.096	2.600±.062
♀CY-2	2.412±.130	3.000±.246	2.565±.119
♀CYs	2.403±.053	2.840±.101	2.510±.049
All ♀s[1]	2.435±.031	3.048±.064	2.586±.030

[1] Includes 9 females from family 35 not recorded.

lutea produced by females 32 might be considered as due to the fact that the average age of this group was younger, but it was less than 3 days younger in the < 120 day group and 6 days younger for all than the females from family 13 producing the largest numbers of corpora lutea. Also in the females of family 32 conceiving over 120 days small corpora lutea counts were observed. Comparison of family 13 and 32 females showed that there were .527 ± .112, 1.179 ± .287, and .698 ± .092 less corpora lutea respectively in the < 120, > 120 and all age groups produced per pregnancy by family 32 females, the differences all being more than three times the probable error, and in case of all females over 7 times its probable error. The same differences between the corpora lutea per pregnancy in females of families 2 and 32 were .379 ± .100, .293 ± .230 and .432 ± .091. The differences for those < 120 days and for all females are also significant, but some allowance must be made in the comparison of the females of all ages for the fact that those of family 2 averaged 35 days older than those of family 32. Allowing 1-3/4 twenty day periods with a regression of .0865 per period, the difference for all ages is reduced to .281, which is approximately 3 times its probable error.

Family 13 females also produced more corpora lutea than females of family 2, the differences in the 3 groups being .148 ± .113, .886 ± .233 and .266 ± .088. The last two are more than three times the probable errors and when allowance is made for age, the differences become greater. The corpora lutea produced by B females were similar to the numbers for the family 2 females except for the group > 120 days; and

to the combined inbreds. Allowing for the younger ages of the B females makes the agreement closer in the < 120 day and all age groups. Corpora lutea production by the CY-O females, which results from crossing family 2 with 13, is curiously lower than either family. The conception age is similar to 13 females but the size of litter is smaller than for those of ♀ 2 but not significantly so when allowance is made for the differences in the age at conception. The CY-1 and CY-2 females averaged slightly older at breeding but they also produced more ova, tho the differences were under 3 times the probable error for all except the > 120 day group for which the numbers from family CY-O and CY-2 were particularly small.

PRENATAL MORTALITY.- Considering the number of corpora lutea observed as representing the number of ova produced, the prenatal mortality is the difference between the number of corpora lutea and the number of normal foetuses observed. The mortality according to this definition may be readily divided into 2 parts, i. e., missing ova and dead foetus; the latter including those cases of so called resorptions and other abnormal cases in which death had obviously occurred.

For the females from all families and in all matings there were 8.70 ± .64 per cent of the corpora lutea for which no embryos or resorptions were found and there were 7.89 ± .61 per cent of the corpora lutea represented by dead foetuses and resorptions. There were 7.60 ± .86 per cent missing ova and 7.83 ± .87 per cent dead foetuses in the left side and 9.77 ± .96 per cent missing ova and 7.96 ± .87 per cent dead foetuses

in the right side. As the difference in the percentages of missing ova in the two sides was largely due to the difference in one family of females, its significance will be discussed later.

The group of dead foetuses was extremely variable in character, ranging from a few large foetuses, almost full term, which showed an extreme dropsical condition, with all of the tissues and abdominal cavity being swelled and filled with fluid, and relatively large embryos from which the soft tissues were largely resorbed, leaving mainly the skeletal parts and skin in a greater or less macerated or mummified condition, to small bodies resembling small placentae except that they were white in color as contrasted with the usual normal dark red color. This type is here described as the button type of resorption, because the placental portion had some resemblance to a thick button. The usual fluids associated with small embryos were largely resorbed, but the membranes remained and in some cases remnants of small embryos were distinguished mainly by the eyes, and frequently the arm buds were observed. The button type of resorption was by far the most frequent type of dead foetuses found. There was still an earlier stage of resorption observed which consisted of a remnant of the deciduum only.

The varied character of dead foetuses indicates that foetuses may die at any time in the gestation period, and it, therefore, seems logical to conclude that the ova of which there were no trace represented not only ova which were imperfect and, therefore, were not normal for fertilization, but also zygotes which died at a very early age and the embryos and membranes were completely resorbed, either before implanta-

tion or at a very early age after implantation. The fact that by far the greater portion of the dead foetuses found were of the button type indicates that mortality is heavier in the young embryos than for those at advanced ages of gestation. From this larger numbers would be expected in the missing ova group. Such appears to be the case, as there were approximately as many missing ova as there were dead foetuses found. It may be concluded, therefore, that the missing ova simply represent, to a large extent, complete resorption.

The data for prenatal mortality are given separately for the missing ova and for the dead foetuses as this is a ready basis for distinguishing between the relative age at which death has occurred, the dead foetuses includes those dying from approximately 15 to 60 days in gestation. From a study of the embryos and comparison and observation of all the data it appears that complete resorption occurs in young dying before the 12th to 20th day of gestation, at which stage implantation has hardly occurred. Remnants of absorption at the younger stages were, of course, much more likely to be missed.

Family differences in prenatal mortality.- Tables 6, 7, and 8 give the percentages of missing ova, dead foetuses, and missing ova and dead foetuses combined in the different types of matings. There is much variation in the percentages observed. Several showed no mortality of ova or foetuses, while among ova produced by females of family 13 over 120 days of age which were mated with males from family 35 there was 50 per cent mortality. All family 13 females mated with males from family 35 showed a mortality of 42 per cent of the ova. There was 57 per cent mortality of the ova produced by CY-2 females, < 120 days, mated with family 35 males. With the exception of the matings with males from family 35 the maximum mortality was between 25 and 30 per cent. The small numbers in any particular type of mating make the probable errors very large and differences of no significance.

Differences in the amount of prenatal mortality would not be expected to show up in the crosses made, even tho true family differences existed. Family 2 and 13 offer the only opportunity for such a comparison. The percentage of missing ova shows considerable differences; in family 2 there were no missing ova, while in family 13 13.79 ± 4.33 per cent of the ova were missing. In dead foetuses there was no difference, 5.26 ± 2.44 and 6.90 ± 3.17 per cent respectively. In total mortality there was also considerable difference, i. e. 5.26 ± 2.44 per cent in family 2 and 20.69 ± 5.05 for family 13, but as is quite evident, the small numbers in each mating make the differences insignificant.

Table 6

Missing Ova in Different Matings

Family of Females	Male Pens ♂ 2			♂ 13			♂ 32			♂ 35			♂ 39			Total females from each family.		
	Age at conception <120 days (per cent)	Age at conception >120 days (per cent)	Total (per cent)	Age at conception <120 days (per cent)	Age at conception >120 days (per cent)	Total (per cent)	Age at conception <120 days (per cent)	Age at conception >120 days (per cent)	Total (per cent)	Age at conception <120 days (per cent)	Age at conception >120 days (per cent)	Total (per cent)	Age at conception <120 days (per cent)	Age at conception >120 days (per cent)	Total (per cent)	Age at conception <120 days (per cent)	Age at conception >120 days (per cent)	Total (per cent)
♀ 2	0	0	0	11.76	7.14	9.68	0	0	0	0	6.67	5.00	10.00	0	8.11	4.90	3.17	4.24
♀ 13	10.00	16.67	11.11	16.67	0	13.79	4.00	20.00	10.00	22.22	16.67	20.83	23.53	7.69	16.67	14.66	13.33	14.29
♀ 32	13.33	-	13.33	18.75	0	15.00	7.69	11.11	9.09	5.26	20.00	8.33	8.00	-	8.00	10.11	11.11	10.28
♀ 35	0	-	0	-	0	0	0	0	0	-	0	0	-	0	0	0	0	0
♀ Inbreds	6.25	9.09	6.59	15.79	3.85	12.05	3.45	8.16	5.61	11.90	10.00	11.11	12.50	3.85	10.20	9.84	6.90	8.91
♀ B	12.00	0	10.34	0	16.67	6.90	14.29	33.33	17.65	5.26	14.29	7.69	0	12.50	8.33	7.44	16.22	9.49
♀ CY-0	12.50	-	12.50	0	0	0	9.09	-	9.09	0	-	0	0	-	0	4.17	0	3.70
♀ CY-1	4.55	25.00	10.00	6.25	0	3.23	0	15.38	6.90	4.55	0	4.17	11.11	0	7.41	5.21	8.51	6.29
♀ CY-2	27.27	0	21.43	0	33.33	20.00	22.22	0	14.29	14.29	0	9.09	10.00	-	10.00	17.07	11.11	15.25
Total CYs	12.20	16.18	13.46	3.70	7.41	5.55	8.33	11.11	9.26	5.00	0	4.35	7.69	0	6.25	7.57	8.45	7.81
Total ♀ s	8.90	11.54	9.30	9.90	7.69	9.04	7.38	10.96	8.72	7.92	9.30	8.33	8.96	4.65	7.91	8.70	8.70	8.70

Table 7

Dead Foetuses in Different Matings

Family of Females	Male Pens ♂ 2 Age at conception <120 days	♂ 2 Age at conception >120 days	♂ 2 Total	♂ 13 Age at conception <120 days	♂ 13 Age at conception >120 days	♂ 13 Total	♂ 32 Age at conception <120 days	♂ 32 Age at conception >120 days	♂ 32 Total	♂ 35 Age at conception <120 days	♂ 35 Age at conception >120 days	♂ 35 Total	♂ 39 Age at conception <120 days	♂ 39 Age at conception >120 days	♂ 39 Total	Total females from each family Age at conception <120 days	Total females from each family Age at conception >120 days	Total females from each family Total
	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent
♀ 2	6.06	0	5.26	17.65	0	9.68	28.57	9.09	16.67	40.00	13.33	20.00	3.33	14.29	5.41	11.76	7.94	10.30
♀ 13	6.67	0	5.55	8.33	0	6.90	0	0	0	16.67	33.33	20.83	0	15.38	6.67	6.03	8.89	6.83
♀ 32	0	-	0	6.25	0	5.00	0	11.11	4.55	10.53	0	8.33	4.00	-	4.00	4.49	5.56	4.67
♀ 35	0	-	0	-	0	0	0	0	0	-	0	0	-	16.67	16.67	0	5.26	3.70
♀ Inbreds	5.00	0	4.40	10.53	0	7.23	6.90	6.12	6.54	16.67	13.33	15.28	2.78	15.38	6.12	7.30	7.59	7.39
♀ B	8.00	0	6.90	0	8.33	3.45	3.57	33.33	8.82	10.53	28.57	15.38	0	0	0	5.79	13.51	7.59
♀ CY-0	0	-	0	0	16.67	7.69	9.09	-	9.09	9.09	-	9.09	0	-	0	4.17	16.67	5.56
♀ CY-1	4.55	0	3.33	31.25	0	16.13	12.50	0	6.90	4.55	0	4.17	16.67	0	11.11	13.54	0	9.09
♀ CY-2	9.09	0	7.14	0	0	0	22.22	0	14.29	42.86	0	27.27	10.00	-	10.00	17.07	0	11.86
Total ♀ CYs	4.88	0	3.85	18.52	3.70	11.11	13.89	0	9.26	12.50	0	10.87	10.26	0	8.33	11.89	1.41	8.98
Total ♀ s	5.48	0	4.65	10.89	3.08	7.83	8.20	6.85	7.69	13.86	13.95	13.89	4.48	9.30	5.65	8.37	6.72	7.89

Table 8

Dead Foetuses and Missing Ova Combined

in Different Matings

Family of ♀ Females	Male Pens: ♂ 2 Age at conception <120 days	♂ 2 Age at conception >120 days	♂ 2 Total	♂ 13 Age at conception <120 days	♂ 13 Age at conception >120 days	♂ 13 Total	♂ 32 Age at conception <120 days	♂ 32 Age at conception >120 days	♂ 32 Total	♂ 35 Age at conception <120 days	♂ 35 Age at conception >120 days	♂ 35 Total	Total females from each family: ♂ 39 Total	♂ 39 Age at conception <120 days	♂ 39 Age at conception >120 days	♂ 39 Total	Total from each family Age at conception <120 days	Total from each family Age at conception >120 days	Total from each family Total
	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent
♀ 2	6.06	0	5.26	29.41	7.14	19.35	28.57	9.09	16.67	40.00	20.00		25.00	13.33	14.29	13.51	16.67	11.11	14.55
♀ 13	16.67	16.67	16.67	25.00	0	20.69	4.00	20.00	10.00	38.89	50.00		41.67	23.53	23.08	23.33	20.69	22.22	21.12
♀ 32	13.33	-	13.33	25.00	0	20.00	7.69	22.22	13.64	15.79	20.00		16.67	12.00	-	12.00	14.61	16.67	14.95
♀ 35	0	-	0	-	0	0	0	0	0	-	0		0	-	16.67	16.67	0	5.26	3.70
♀ Inbreds	11.25	9.09	10.99	26.32	3.85	19.28	10.34	14.29	12.15	28.57	23.33		26.39	15.28	19.23	16.33	17.14	14.48	16.30
♀ B	20.00	0	17.24	0	25.00	10.34	17.86	66.67	26.47	15.79	42.86		23.08	0	12.50	8.23	13.22	29.73	17.09
♀ CY-0	12.50	-	12.50	0	16.67	7.69	18.18	-	18.18	9.09	-		9.09	0	-	0	8.33	16.67	9.26
♀ CY-1	9.09	25.00	13.33	37.50	0	19.35	12.50	15.38	13.79	9.09	0		8.33	27.78	0	18.52	18.75	8.51	15.38
♀ CY-2	36.36	0	28.57	0	33.33	20.00	44.44	0	28.57	57.14	0		36.36	20.00	-	20.00	34.15	11.11	27.12
Total ♀ CYs	17.07	18.18	17.31	22.22	11.11	16.67	22.22	11.11	18.52	17.50	0		15.22	17.95	0	14.58	19.46	9.86	16.80
Total ♀ s	14.38	11.54	13.95	20.79	10.77	16.87	15.57	17.81	16.41	21.78	23.26		22.22	13.43	13.95	13.56	17.07	15.42	16.59

A comparison of the mortality among ova produced by all the females of particular families and all the females of several families mated with males from a particular family was made. Considering first the mortality in the different male pens as given in Table 9, the percentage of missing ova ranges from 7.91 ± 1.37 per cent for ♂ 39 to 9.30 ± 1.49 per cent for ♂ 2, the maximum difference being less than its probable error, and therefore not significant.

The variation in the percentage of dead foetuses is considerably greater, ranging from 4.65 ± 1.08 per cent for ♂ 2 matings to 13.89 ± 1.94 per cent for ♂ 35 matings. The mortality of foetuses in ♂ 39 matings is low, 5.65 ± 1.17 per cent, not differing significantly from ♂ 2 matings, 4.65 ± 1.08 per cent, while it is very close to the average in ♂ 13 and ♂ 32 matings. The striking feature is the high mortality among the foetuses of all females mated with males of family 35, 13.89 ± 1.94 per cent. The foetal mortality makes the total mortality higher in ♂ 35 matings than in ♂ 2 or ♂ 39 matings, the respective differences being 8.27 ± 2.93 and 8.66 ± 3.07 per cent. These differences only approach significance. Obviously none of the other differences are significant. A study of the mortality of ova from the females of the different families in ♂ 35 shows that they are practically all high wherever the numbers of females are sufficiently large to be representative. The total mortality is as follows for the females from the following families in ♂ 35 matings: ♀ 2 25.00 per cent, ♀ 13 41.67 per cent, ♀ 32 16.67 per cent, ♀ Inbreds 26.39 per cent, ♀ B 23.08 per cent, ♀ CYs 15.22 per cent. The only exceptions to this are in ♀ 35 of which there was only 1 female and ♀ CY-O and ♀ CY-1, of which there

Table 9.

Prenatal Mortality in Different Male Pens

Male Pens	Missing Ova	Dead Foetuses	Dead foetuses and missing ova
	per cent	per cent	per cent
2	9.30 ± 1.49	4.65 ± 1.08	13.95 ± 1.78
13	9.04 ± 1.50	7.83 ± 1.39	16.87 ± 1.96
32	8.72 ± 1.36	7.69 ± 1.29	16.41 ± 1.79
35	8.33 ± 1.55	13.89 ± 1.94	22.22 ± 2.33
39	7.91 ± 1.37	5.65 ± 1.17	13.56 ± 1.73
Total	8.70 ± .64	7.89 ± .61	16.59 ± .85

were 4 and 10 females respectively, the latter being nearly as many females as there were of any particular family in any mating. The percentage of dead foetuses differed significantly between ♂ 35 and ♂ 2 and ♂ 39 pens. These differences were respectively 9.24 ± 2.22 and 8.24 ± 2.27. The difference in per cent dead foetuses between ♂ 35 and ♂ 32 is 6.20 ± 2.33 per cent or 2.66 times its probable error, and between ♂ 35 and ♂ 13 is 6.06 ± 2.39 or 2.53 times its probable error. Other differences are not possibly significant. Since the foetal mortality in ♂ 35 matings is relatively high, it must be concluded that the high percentage of dead foetuses in these matings is due to something transmitted by males of family 35.

As in the male pens, there was much variation in the prenatal mortality in the female families. Table 10. In contrast to the male pens, in which the percentage of missing ova was relatively uniform, the females show more variation in this respect than in the percentage of dead foetuses. There were the largest percentages of missing ova in ♀ CY-2 and ♀ 13, 15.25 ± 3.16 per cent and 14.29 ± 1.86 per cent respectively, and the smallest percentages of missing ova in ♀ CY-O and ♀ 2, 3.70 ± 1.73 per cent and 4.24 ± 1.06 per cent respectively. There were no missing ova in ♀ 35, but the small number of females make this rather unreliable. The difference between the two inbred families ♀ 13 and ♀ 2 is 10.05 ± 2.14 per cent and between ♀ CY-2 and ♀ CY-O is 11.55 ± 3.60 per cent. There are significant differences between ♀ 35 and all other families except ♀ CY-O, though the numbers of family 35 females are very small. Several of the other differences approach significance, but none are clearly significant. It is, however, clear that there are significant family differences in the percentage

of missing ova, larger amounts occurring in ♀ CY-2 and ♀ 13 than in ♀ CY-0 and ♀ 2.

The largest percentage of dead foetuses were also observed in ♀ CY-2, 11.86 ± 2.84 per cent, but ♀ 2, which had a low percentage of missing ova, had 10.30 ± 1.60 per cent of dead foetuses. Except for ♀ 35, of which there were few females, the lowest percentages of dead foetuses were observed in ♀ 32 and ♀ CY-0, 4.67 ± 1.38 and 5.56 ± 2.10 per cent. The maximum difference here is between ♀ CY-2 and ♀ 32, 7.19 ± 3.16 per cent, and between ♀ 2 and ♀ 32, 5.63 ± 2.11 per cent, neither of which are significant. The differences between ♀ 35 and ♀ CY-2 and ♀ 2 respectively were 8.16 ± 3.75 per cent and 6.60 ± 2.93 per cent. Thus several of the differences in the percentage of dead foetuses approached significance, but none can be said to indicate true differences.

In total prenatal mortality ♀ CY-2 excelled all others, there being 27.11 ± 3.91 per cent of the ova observed as missing ova and dead foetuses; and ♀ CY-0, which was relatively low in the percentages of missing ova and dead foetuses, was obviously low in total prenatal mortality, being excelled only by ♀ 35, in which the total prenatal mortality was only 3.70 ± 2.45 per cent, but which is subject to the criticism of small numbers. The differences between families which were greater than three times the probable error were: ♀ CY-2 and ♀ CY-0, 17.85 ± 4.73 per cent; ♀ CY-2 and ♀ 35, 23.41 ± 4.61 per cent; ♀ 13 and ♀ 35, 17.51 ± 3.27 per cent, ♀ 13 and ♀ CY-0, 11.95 ± 3.43 per cent; ♀ 32 and ♀ 35, 11.25 ± 3.38 per cent, ♀ 2 and ♀ 35, 10.84 ± 3.07 per cent; ♀ CY-1 and ♀ 35

Table 10

Prenatal Mortality in the Different Female Families.

Females Family	Missing ova			Dead Foetuses			Missing ova and dead foetuses		
	Left cornu	Right cornu	Total	Left cornu	Right cornu	Total	Left cornu	Right cornu	Total
	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent
2	5.38	2.78	4.24 ± 1.06	12.90	6.94	10.30 ± 1.60	18.28	9.72	14.54 ± 1.85
13	9.76	18.99	14.29 ± 1.86	4.88	8.86	6.83 ± 1.34	14.64	27.85	21.21 ± 2.17
32	11.11	9.68	10.28 ± 1.98	2.22	6.45	4.67 ± 1.38	13.33	16.13	14.95 ± 2.33
35	0	0	0	7.69	0	3.70 ± 2.45	7.69	0	3.70 ± 2.45
Inbreds	7.73	10.13	8.91 ± .90	7.73	7.05	7.39 ± .82	15.46	17.18	16.30 ± 1.16
B	9.33	9.64	9.49 ± 1.57	8.00	7.23	7.59 ± 1.42	17.33	16.87	17.08 ± 2.01
CY-0	3.45	4.00	3.70 ± 1.73	3.45	8.00	5.56 ± 2.10	6.90	12.00	9.26 ± 2.66
CY-1	7.04	5.56	6.29 ± 1.37	8.45	9.72	9.09 ± 1.62	15.49	15.28	15.38 ± 2.04
CY-2	7.69	21.21	15.25 ± 3.16	11.54	12.12	11.86 ± 2.84	19.23	33.33	27.11 ± 3.91
All CYs	6.35	9.23	7.81 ± 1.13	7.94	10.00	8.98 ± 1.21	14.29	19.23	16.79 ± 1.42
All Families	7.60	9.77	8.70 ± .64	7.83	7.96	7.89 ± .61	15.43	17.73	16.59 ± .85

11.68 ± 3.19; ♀ B and ♀ 35, 13.38 ± 3.17 per cent. Thus if dependence can be placed in the small numbers of females in ♀ 35 matings, the total mortality is significantly less than that observed in all the female matings except ♀ CY-O.

The fact that there were significant differences in the percentage of missing ova in the matings of the females of particular families with males from all the families, but no significant differences in the percentage of dead foetuses, and the converse occurred when grouped according to male pens, i. e., there were no significant differences in the missing ova, but significant differences in the percentage of dead foetuses seems to have a definite meaning. Consider first the results for the male matings. There is evidently nothing which the males contribute in their sperm which influences the percentage of missing ova in which the families differ. On the other hand, sperm produced by the different families vary in the percentage of dead foetuses which result. It therefore may be considered that if sperm are abnormal (carry lethal factors), they are sufficiently normal to cause fertilization and result in the initial development of the zygote, and it therefore develops to the point where it is recognized as a dead foetus. The mortality of female gametes as well as zygotes is being determined by the method employed. Evidently the missing ova approximate the mortality of ova in which families differ and with which the male is not concerned. These data furnish no evidence of the mortality of the sperm, which unless very heavy is not an important factor in fertility. The variation in the dead foetuses resulting from the sperm influence is the outcome of a normal ovum mating with a

normal sperm but carrying some lethal factor which acts on the developing embryo at a sufficiently late stage in development so that the embryo is found as a resorption. It would be expected that the ovum would be just as likely to carry lethal factors as the sperm and the variability in the percentage of dead foetuses in the different female families gives indication of such, tho the differences are not significant. It should be mentioned that if lethal factors are carried by the male, as is indicated above, they could hardly operate in a simple manner, since their evidence would not be expressed in the first generation unless they were dominant or were carried by both families. If they were dominant the male (sire) could not itself exist. Such lethal effect could only be expressed as the result of a definite balance between several factors. There is also probability of other than genetic factors in the zygote playing a part, such as the size and physiological condition of the dam, number of embryos per litter, etc., tho the male can only be responsible thru its contribution in the spermatozoan which fertilizes a particular ovum. Other possibilities will be discussed below.

Relation of distribution in the uterus to prenatal mortality.- The mortality for all embryos in the left and right horns of the uterus did not differ significantly. There were 7.60 ± .86 per cent missing ova and 7.83 ± .87 per cent dead foetuses in the left cornu and 9.77 ± .96 per cent missing ova and 7.96 ± .87 per cent dead foetuses in the right cornu. In the particular families

Table 11.

Relation of Size of Litter to Prenatal Mortality

Size of Litter	Missing Ova	Dead Foetuses	Total Prenatal Mortality
	per cent	per cent	per cent
1	0✓	0✓	0✓
2	5.00 ± .82	5.00 ± .82	10.00 ± 1.13
3	11.83 ± 1.13	10.22 ± 1.06	22.04 ± 1.45
4	10.61 ± 1.81	9.85 ± 1.75	20.45 ± 2.37
5	3.33 ± 2.21	6.67 ± 3.07	10.00 ± 3.69
6	16.67 ± 10.26	0	16.67 ± 10.26
Difference 2 and 3	6.83 ± 1.40	5.22 ± 1.34	12.04 ± 1.84

✓ No mortality in litters of one could have been discovered.

there was some irregularity, especially in the missing ova, the percentages in the left and right differing by 13.52 ± 5.95 per cent in ♀ CY-2. In only one other family, ♀ 13, does the difference approach significance. There is, therefore, no evidence of a greater percentage of missing ova in one side than in the other, and there is even less evidence of differences between the two cornu in the percentage of dead foetuses observed.

The relation of the amount of prenatal mortality to the size of litter or number of corpora lutea produced as given in table 11 offers an interesting study. For reasons already given cases of prenatal mortality in litters of one could not have been discovered, and therefore the zero value for this litter size. There is evidently a significant difference in the per cent missing and per cent dead foetuses observed in litters of 2 and litters of 3, but litters of 4 show almost the same mortality as litters of 3, and there were too few litters of 5 and 6 to be of much account.

Calculation of the mortality in one cornu when the number of ova produced by the other ovary was constant, as given in table 12, showed some evidence of association between mortality and the number of ova in the same side, but here again this relation only held when the numbers in the constant side were 0 and 1. In these cases it held equally for the percentage of missing ova and dead foetuses, but with the constant litter size of 2 opposite relations were shown. The latter differences were, however, not significant.

Position of dead foetuses in uterus.- The finding of a few of the dead foetuses implanted in the anterior tip of the cornu of the uterus

Table 12

Prenatal Mortality in One Cornu with Ova in other side constant.

Constant number of ova in one side	Number of ova in other side	Missing ova	Dead foetuses	Total prenatal mortality
		per cent	per cent	per cent
0	2	7.41 ± 1.39	4.32 ± 1.08	11.73 ± 1.71
0	3	14.29 ± 2.58	10.71 ± 2.27	25.00 ± 3.18
0	4	0	16.67 ± 5.13	16.67 ± 5.13
1	1	2.53 ± .84	5.70 ± 1.24	8.23 ± 1.48
1	2	9.38 ± 1.42	13.02 ± 1.64	22.40 ± 2.03
1	3	19.44 ± 4.45	19.44 ± 4.45	38.88 ± 5.48
2	1	8.33 ± 1.90	10.42 ± 2.10	18.75 ± 2.68
2	2	6.67 ± 2.17	5.00 ± 1.90	11.67 ± 2.79
2	3	11.11 ± 5.00	5.56 ± 3.64	16.67 ± 5.92
2	4	0	0	0
3	1	16.67 ± 7.26	0	16.67 ± 7.26
3	2	0	0	0
4	2	0	50.00 ± 23.85	50.00 ± 23.85

or very near the body of the uterus suggested a possible relation of the position of implantation to the mortality of the foetuses. In extreme cases a note was made about the position of implantation, but no comment was made on the original record sheet when the implantation was reasonably normal. Therefore, in cases in which the dead foetus was the only foetus present in one cornu and in which its position of implantation was reasonably within the major portion of the expansive portion of the cornu, there was no basis for defining its position. In cases of two or more foetuses in 1 cornu they could be distinguished as No. 1 and No. 2, etc., beginning from the anterior end of the cornu and counting posteriorly.

Among the 69 dead foetuses found in all females there were 17 from 14 family 2 dams, 11 from 9 family 13 dams, 5 from 4 family 32 dams, 1 from 1 family 35 dam, 12 from 10 family B dams, 3 from 3 family CY-0 dams, 13 from 11 family CY-1 dams, and 7 from 4 family CY-2 dams. In six of the pregnancies there were dead foetuses in both cornua of the uterus, in five pregnancies there were 2 dead foetuses in the same cornu, and in one pregnancy there were 3 dead foetuses in one cornu.

There were 18 of the dead foetuses which were located alone in the cornu as the only foetus present. One each in females from families 13, B and CY-1 was in the posterior third of the cornu. The others were all regularly attached in the mid portion.

There were 34 dead foetuses in 33 cornu which contained 2 foetuses. Of these there was one cornu in which both foetuses had died. Of the other 32, 20 were in the anterior position and 12 were in the posterior

position; the normal foetus associated with them thus being more frequently in the posterior position.

There were 17 dead foetuses in 11 cornu containing 3 foetuses. In one of these all three were dead. In one each the first and third and the second and third were dead, while in two others the first and second were dead. In four cornua the first only and in two cornua the third only were dead. The second and third positions thus seem slightly more favorable than the first position for normal development.

When all the data are grouped together for cornua in which there were two or three foetuses there are 29 embryos which were in the first position, i. e., nearest the Fallopian tube, and 18 which were in the last position, i. e., nearest the body of the uterus. If conditions of mortality were equal there would be expected 23.5 in each position, making a difference between the observed and calculated in each instance of 5.5, giving a value for X^2 of 2.58. For 1 degree of freedom such a distribution would be expected to occur about 11 times in 100 trials. Other methods of calculating the significance give similar or slightly larger probabilities.

The numbers are so small in which the cornua containing three foetuses are involved that they do not warrant further discussion, but it is interesting for those cornua containing 2 foetuses that when separated according to the females, family CY-O and CY-1 show an equal distribution, and there were none in CY-2; family 32 and 35 show a greater mortality of the posterior embryos, while family 2, 13 and B in which there were distinctly larger numbers, showed a considerably

greater mortality of those in the anterior position, 16 to 5 in these three families combined. The value of X^2 in this case was 5.76, which would be expected less than twice in 100 trials.

The data as a whole points toward a greater mortality of embryos in the most anterior position in the uterus, tho they cannot be said to positively prove that such is the case. Certainly location in the anterior end of the cornu does not account for all cases of prenatal mortality, and there is no doubt of the action of a more fundamental factor or association of conditions which considerably complicates the situation.

For convenience, the numbers of dead foetuses found in different positions in cornu containing two and three foetuses are summarized as follows:

Position	Number of dead foetuses in each position		
	Cornua containing 2 foetuses	Cornua containing 3 foetuses	Total
Nearest Fallopian Tube (No. 1)	21	8	29
Nearest Body of Uterus (No. 2 or No. 3)	13	5	18
No. 2 in cornu with 3 foetuses		4	4

Seasonal variation in prenatal mortality.- Table 13 gives the mean corpora lutea count per litter conceived in the different months, as well as the prenatal mortality in the litters conceived in each month, and the mean number of normal foetuses.

The seasonal fluctuation in size of litter as measured by both the ova and the number of normal embryos per litter agrees fairly well with the findings in Part I for litter size. There the litter size was given for the month of birth and the most favorable months were July and August. The number of ova and normal embryos are given for the month of conception and the high months are April, May and June, with a second mode in December. The latter is not in accord with anything observed in the larger body of data, but advancing the mode of April, May and June sufficiently to take account of the gestation period, this mode corresponds closely.

The low period for the size of litter in the smaller group of data was for conceptions in August, September and October, while the smallest litter sizes were observed in the larger body of data for those litters born in the late winter and early spring.

It is not surprising that the two groups of data do not show uniformity, as the study of the larger body of data was based on a combination of 18 years records, each year of which showed individual seasonal variation. It is hardly to be expected that the smaller group of data collected in about 15 months should agree precisely with the average for that period. Further, the fact that first litters were selected for the experimental work may account for some differences in behavior.

Table 13.

Monthly Variations in Litter Size and Prenatal Mortality.

	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
Number of litters	38	31	26	14	24	38	20	16	35	22	38	36	338
Mean number of corpora lutea	2.55	2.58	2.58	2.93	2.79	2.89	2.60	2.25	2.26	2.09	2.55	2.83	2.586 ± .030
Per cent missing ova	11.34	6.25	1.49	9.76	10.45	11.82	9.62	13.89	10.13	2.17	8.25	7.84	8.70 ± .64
Per cent dead foetuses	8.25	15.00	17.91	7.32	1.49	2.73	9.62	0	8.86	15.22	8.25	2.94	7.89 ± .61
Per cent prenatal mortality	19.59	21.25	19.40	17.08	11.99	14.55	19.22	13.89	18.99	17.39	16.50	10.78	16.59 ± .85
Mean number of normal foetuses	2.05	2.03	2.08	2.43	2.46	2.47	2.10	1.94	1.83	1.73	2.13	2.53	2.157 ± .032

There is a tendency to a high degree of total prenatal mortality for litters conceived in January, February and March, with other high points in July and September. The most favorable month was May. On the whole, however, the variations were not great considering the small numbers of litters conceived in each month, the minimum being practically 12 per cent in May and the maximum 21.25 per cent in February. Five of the twelve months were practically 19 per cent or above, i. e., January, February, March, July and September.

In contrast with the relatively small amount of variability in total prenatal mortality there was a great deal of variation in the percentages of missing ova and percentage of dead foetuses. The missing ova varied from 1.49 per cent to 13.89 per cent, and the dead foetuses from 0 to 17.91 per cent. Curiously enough there was a reciprocal relation between the percentages of missing ova and dead foetuses. For instance, there were 17.91 per cent dead foetuses in March but only 1.49 per cent missing ova in this month. There was a similar relation in October and in May, June and August the percentages of missing ova were high and the percentage of dead foetuses low. It is possible that missing ova and dead foetuses are not due to entirely different causes but slight variations in the cause may modify the time at which the death of the embryos occurs and the rapidity at which resorption goes on. There is a possible indication that large percentage of dead foetuses is associated with the period just before larger litters are conceived, while a greater tendency toward missing ova is associated with the period just before the conception of small litters, but the small group of data make this of questionable significance.

Types of dead foetuses.- There was a total of 69 dead foetuses of which remnants were found varying from decidua only to large foetuses which appeared fully developed except that their bodies were very edematous. An effort was made to group them according to five different types, which was based on the stage to which they had developed and the degree to which resorption had advanced after death. These types were designated as decidua, button, small, large and mummy. The decidua type refers to those cases in which resorption had progressed so far that nothing remained but the deciduum basalis, all traces of the embryo, membranes and placenta having disappeared. The button type refers to those cases in which the embryo had died at a relatively early age and the embryo and membranes and fluids were shrunken and resorbed with a considerable shrinking and toughening of the placenta. Such placentae were usually light in color with a dark spot on the top where the foetal membranes attached. Frequently the foetus could be identified in the shrunken membranes. It was estimated that the foetuses in this type did not develop beyond the 20th day of gestation.

Those cases in which the foetus could be definitely recognized but which were less than approximately half as large as the normal foetuses were classed as small foetuses. These were usually dark in color and some had petichae over the surface of the body. Some of these apparently died as the result of hemorrhage between the placenta and deciduum, which was relatively common in the small, large and mummified groups. In all there were ten cases of this type of hemorrhage. There were a few large or mummified foetuses which had evidently developed to a rather advanced

stage of gestation and succumbed because of hemorrhage from the placenta or because of edema in the embryo. The numbers of each type of dead foetus found in the females of the different families were as follows:

Females Family	Decidua	Button	Small	Large	Mummy
2	6	6	2	2	1
13	1	5	2	3	
32	2	2	1		
35		1			
B	3	7	2		
CY-0		1	2		
CY-1	5	2	5		1
CY-2	1	6			
Totals	18	30	14	5	2

Two of the large foetuses were edematous, one in a female from family 2 from the 39 male pen and the other from a family 32 female mated with a family 32 male. The rest of the large foetuses were mummies, and five of the small foetuses showed hemorrhagic placentae. The possibility of the necessary handling involved in the diagnosis of the stage of pregnancy immediately suggests itself as a cause of the placental hemorrhage by partially tearing it from its deciduum, but this condition was as frequently found in dams not included in this experiment which were not so handled, but which were posted after natural death. The edematous type of foetus was also found among those individuals. Attention has been called to the hemorrhagic condition by others; for instance, Kelly (1908) gives one of the causes of abortion in women as Hemorrhage of the chorion.

It is interesting to note that the greater amount of prenatal mortality in the guinea pig seems to occur before the 20th day of gestation. Of the 874 corpora lutea found there was no evidence of 76 and 48 died before the 20th day of gestation, while the balance, 21, died at more advanced ages. The death of the last was mainly due to hemorrhage between the placenta and deciduum or to some abnormality in development, such as the edematous condition. One otocephalus individual was also found which was perfectly normal as far as its development was concerned, but could not have lived long after birth. Its condition was perfectly normal, and it was not counted as a dead foetus.

It is generally considered that prenatal mortality falls heavier on the male embryos than on female embryos, as found in rats by Miss King (1921 and 1927) and in mice by Parkes (1926), and as has been observed in numerous cases of still births in man and other animals. Riddle (1927) gave as the explanation, the fact that male embryos developing in the uterus of the dam and subject to the female hormones are constantly in an unfavorable environment. On the other hand MacDowell and Lord (1926) found no continuous selective elimination of one sex or the other in utero from a study of 840 litters in mice.

It was possible to determine the sex of only 8 of the dead foetuses and of these four were males and four females. In the cornua in which dead foetuses were found there were 59 normal foetuses of which the sex was determined. These were 26 males and 23 females. While these data are insufficient as a basis for any conclusions, they do not indicate a greater degree of prenatal mortality of one sex than of the other.

Discussion

Variation in the age at conception resulting in pregnancy was noted between the females of certain families when all were allowed to mate with males from 33 days of age on. The striking feature of these differences was the part played by the males. It clearly shows that age at which a fertile conception occurs can not be accurately used as the basis for the attainment of sexual maturity. The use of the vaginal smear method of determining the heat period for such purposes is coming into more customary use, and is no doubt more accurate. The most accurate method seems to be based on histological study of the ovaries and testicles for the production of corpora lutea and mature spermatozoa. Parkes (1925). Male rats were found to copulate by Stone (1924) before mature spermatozoa were present in the tubules of the testes.

The advanced age of conception in certain types of matings, i. e., ♂ 13 and ♀ Cy and the early breeding of CY females in all matings with other males may lend support to the idea of the compatibility and incompatibility of particular matings as Macomber (1923) found in rats.

The number of corpora lutea found in both ovaries of the 338 females varied from 1 to 6 and these were distributed at random between the left and right ovaries, but the total number seemed to be under some central control of the organism. This was shown to be in accord with the hypothesis of Danforth and de Aberle (1928) and the findings of Lipschutz (1925 and 1927), Lipschutz and Voss (1925), Hartman (1925) and Asdell (1924). Hammond (1925) suggested that the proportion of the ova pro-

duced by each ovary in the rabbit depends upon the relative blood supply of each. Hanson and Boone (1926) suggest a reciprocal hormone relationship between the two ovaries in which each one tends to suppress the other, and when one ovary is removed the other hypertrophies and produces as many ova as is normally produced by both ovaries. The method of operation of such reciprocally acting hormones is not clear.

Immaturity in females is generally recognized as conducive to small sized litters in multiparous animals (Marshall (1922). Minot (1891) observed that size of litter in guinea pigs increased with age during the first 16 months. Successive increases in litter size up to the third or fourth litters of dams were also noted in Part I. There seems to be no doubt but that smaller sized litters are produced by females which have just reached sexual maturity than by the same females at a more advanced age. Ibsen (1928) however reported only a small linear correlation between age of dam and size of litter in the guinea pig .18 $\pm$.06, probably because of the decline after a certain age is reached. Wright (1926) found a high correlation between age of dam and parity. When the peak in the reproductive ability is reached there is then a decline in size of litter. As the females in the present study were all less than one year of age, this decline did not enter into the results.

The families ranked in approximately the same order for the numbers of corpora lutea per litter produced in these first litters after making suitable corrections for age as the same families were ranked by Wright (1922) in size of litter. The prenatal mortality is thus dis-

tributed in all the families and is not limited to particular ones, tho the amount of mortality was found to vary to some extent with families, but such variability was not sufficient to modify the rank of the families in size of litter.

Of the 874 corpora lutea found in the 338 females 16.59 ±.85 per cent of the ova were either missing or found as partial resorptions or dead foetuses. This is somewhat less than has been reported for other animals in which the estimates have been as high as 40 per cent. In sheep Hammond (1914) reported a 12.9 per cent mortality of the ova; in the pig Hammond (1921) reported 32.5 per cent and 40 per cent mortality based on different estimates, while Corner (1923) found 23.3 per cent mortality in this animal, and Crew (1925-26) reported 26 per cent of the ova not developing into normal foetuses; in the rabbit Robinson (1921) reported 37.5 per cent mortality, while Biedl et al (1921) found 18.3 per cent and Hammond (1925) found that 20 per cent of the ova shed by outcross does and 62 per cent shed by inbred does failed to produce normal foetuses; in the ferret Robinson (1921) estimated 24.2 per cent reabsorptions from a comparison of the number of normal foetuses found with the corpora lutea counts and 39.2 per cent from a comparison of the average number of corpora lutea with the average size of litter in this animal; in the rat Long and Evans (1922) estimated 33 per cent prenatal mortality from a comparison of the average number of corpora lutea with the average size of litter; in mice Parkes (1923 I) found 9.8 per cent of the ova were not recovered as normal foetuses, and that this might be increased to 15 per cent by breeding within 24 hours after the birth of the previous litters; when there was prolonged suckling this was further in-

creased to 18.8 per cent; Mac Dowell in several papers indicates that from 30 to 40 per cent of the ova shed in mice do not produce living young at birth. MacDowell (1924) and MacDowell et al (1924).

The estimates of the prenatal mortality in different species and by different investigators working with the same species show considerable variations. Part of this is due to differences in the basis for the estimates, some being based on the relation between the number of corpora lutea found and the number of apparently normal embryos in the uterus, while others are based on the relation between the number of corpora lutea found and the average size of litter at birth or number of living young. Obviously the relation of the corpora lutea count to the number of living young born would show a much greater mortality than when the number of normal foetuses serves as the basis, because the one includes the mortality at parturition. The larger estimates mostly include the total mortality. The prenatal mortality in the guinea pig appears to be slightly less than that in many of the other classes of animals. It is not entirely clear why this should be but there are a number of conditions which may have a bearing: (1) The prenatal mortality in the guinea pig is based on first litters which are smaller than subsequent litters. (2) The size of litter is normally smaller than in the other animals considered except the sheep, which also shows a relatively small amount of prenatal mortality. (3) The majority of the embryos were cross bred, which would not be expected to show the effects of recessive lethals carried by particular families. (4) There is a relatively high mortality at birth in the guinea pig which is not included. (5) On the other hand the guinea pig is relatively more mature at birth than most

of the other types and the gestation period is about three times as long as in the other laboratory rodents, giving a longer period over which foetal mortality would be expected to occur.

Investigations of the causes of embryonic mortality have given mainly negative results except as pertains to the lethal factors which have been found to so seriously interfere with development that they cause death of the embryo either before birth or shortly afterward. In this sense the definite positive evidence all points toward a genetic basis. The first case of lethals clearly worked out in mammals was probably that of the yellow mouse. Cuenot (1905), Castle and Little (1910), Ibsen and Steigleider (1917), and Kirkham (1919). Other cases in the mouse have since been noted by Detlefsen (1923) and Little (1916), de Aberle (1924) and others. Numerous cases in the larger mammals have been reported upon in recent years to which attention has been mainly called by Wriedt (1925) for cattle, horses, swine, dogs and poultry.

Besides the indication of variation in the amount of prenatal mortality associated with the season, size of litter and distribution of foetuses in the guinea pig, other investigations have reported positive results bearing on variations in the amount of prenatal mortality. MacDowell and Lord (1927) reduced the size of litters born by 12.3 per cent in mice without influencing the number of corpora lutea produced, by treating the females heavily with alcohol. Parkes (1924 I) increased the mortality of ova in mice from the normal of 9.8 per cent to 15 per cent by breeding immediately after parturition. This was further increased to

18.8 per cent by allowing a long suckling period after breeding.

Most other evidence has been negative. For instance, Asdell (1924) produced a much greater amount of crowding by removing one ovary and producing nearly the normal size of litter in one cornu without significant effect on the prenatal mortality. In a careful histological study of atrophied pig embryos Corner (1923) and Streeter (1923) concluded that the embryonic mortality was not due to faulty implantation or abnormalities in the uterine mucosa. Streeter stated "There is much to indicate that embryos may become abnormal in spite of a uterine environment which by all the criteria at our present command is both anatomically and functionally normal." He further points out "that about 10 per cent of the ova never segment, about 10 per cent degenerate after becoming blastocysts and that 5 to 10 per cent become abnormal during the subsequent course of pregnancy." The many cases in which but one embryo in a litter dies while others subjected to the same intra uterine environment develop normally to maturity bears this out.

When one considers external influences on the dam as influencing embryonic mortality there is first the evidence of MacDowell et al (1924) to refute, in which the operation of etherizing the pregnant female, cutting into the abdominal cavity, counting the corpora lutea in the ovaries and subsequently sewing up the incision had no effect on the number of young born alive or size.of the subsequent litters. How can such minor influences as seasonal variations be a modifying factor?

The fact that shock to the dam does not influence prenatal mortality would indicate that environmental factors - anything aside from

the genotype of the embryo - which affect the mortality of the embryos must act over a considerable time or have a lasting effect. This rather points to nutrition, which would be expected to be gradually less and less adequate to meet the needs of the individual foetus, or crowding which would increase as development proceeded. Inadequate nutrition and crowding are merely suggested, but the middle foetus of three located in the same cornu appears to be lighter in weight and gives added significance to this suggestion.

On the other hand Hammond (1921) in addition to pointing out that foetal atrophy cannot be due to bacterial infection, since the uterus is aseptic, concluded that it could not be due to overcrowding, since the uterus is capable of unlimited expansion and the irregular distribution of degenerate foetuses does not suggest that death is due to overcrowding. Ibsen (1928), however, favors overcrowding as the cause in the guinea pig.

The conclusions of various investigators as to the causes of foetal mortality in animals are largely conflicting. This is no doubt in part due to the fact that many of them are simply efforts to explain conditions found and not based on controlled experiments, partly because there are no doubt several factors or conditions favoring the incidence of foetal mortality and partly because they are based on observations in various types of animals in which the favorable conditions may vary.

There is little information on the nature of absorption of foetuses which die, beyond the numerous references to the fact that the character of the dead foetuses found give evidence that there has been an absorption of the fluid parts of the foetuses. A knowledge of how this process proceeds might throw light on the primary cause of death and the initial steps of

the process. Long and Parkes (1924) made a valuable contribution to this phase by incubating rat and mouse embryos and one pig embryo in sterile Ringer's solution at 37° C. Such embryos were reduced practically to skeletons in seven or eight days. The process seemed to originate in the liver and extend to other parts of the embryo, as well as the placenta and membranes. The disintegration in utero is thought to result from the action of enzymes produced by the embryo and the disintegration of the placenta is slower because of its contact with the maternal tissue. The uterus of the dam simply absorbs the products in solution which consist of amino acids and peptones. This process was shown to go on under sterile conditions and was not the result of bacterial action.

Exceptional Cases

There were thirteen females which showed the presence of greater numbers of normal foetuses plus dead foetuses in one cornu of the uterus than there were corpora lutea in the ovary on that side. These have been designated under this heading.

Before taking up these cases individually it seems proper to call attention to other cases of more foetuses than corpora lutea which have been observed by others and explanations suggested. Corner (1915) found cases of more corpora lutea than foetuses in the pig and Hammond (1921) reported more corpora lutea than foetuses in a few rabbits. Likewise MacDowell and Lord (1925) from similar findings in mice conclude "that there is a possibility of more than one mature ovum for one corpus luteum but again there seems to be no means of judging the possibilities." Corner (1923) states that "Errors might conceivably occur through failure

of corpora lutea to develope in ruptured follicles, the production of supernumerary corpora lutea, the occurrence of polyovular follicles, or the persistence of corpora lutea from earlier ovulations." It seems to be generally agreed that corpora lutea do not form unless the follicle has practically matured, tho the follicle may become atresic and not rupture. If an atresic follicle formed a corpus luteum it would in no way account for larger numbers of foetuses than corpora lutea.

There is evidently some chance of follicles being ruptured without the formation of corpora lutea, at least of the type that continue throughout pregnancy. For example, Mandl (1904) described a case of pregnancy in the rabbit without evidence of a corpus luteum in either ovary.

Hartman (1926) gives an account of the relative frequency of polynuclear ova and polyovular follicles in opossum ovaries but found that the most advanced stages were always atresic and there were no compound structures among the ripe follicles. It is concluded that these structures are not a cause of increased fertility. There remains, however, the possibility of twinning which has been observed in many multiparous animals. Streeter (1924) described a clear cut case in the pig, though Wright (1928) did not find any evidence of twinning in the guinea pig.

Aside from the possibility of only one corpus luteum being formed when more than one ovum is liberated and the possibility of one follicle producing more than one ovum, it is possible that two corpora lutea might be so close together that they would be counted as one. This seems very doubtful as the ovaries were carefully examined a second time when more foetuses than corpora lutea were discovered, and it is hard to understand

how such conditions could exist after examination of the specimens. Many cases of two corpora lutea lying side by side were found and they were always very distinct when sectioned with the scalpel which was the invariable practice.

The corpora lutea of the guinea pig are very distinct in practically all cases in the ovary though there were a few cases in which the color was somewhat darker than normal and less distinct, which was assumed to be the beginning of the regressive changes, which evidently normally set in immediately after parturition. There were also some cases in which dark yellow material was present in the ovaries in small amounts, but these were never as clear cut as the normal corpora lutea of that litter, but were assumed to be corpora lutea remaining from the previous litter. The characteristics were so distinct that there appeared to be no confusion in distinguishing them. Verdozzi and Venni (1926) also pointed out that the corpora lutea of the guinea pig did not show regressive changes during the pregnancy period. It is not impossible to understand how some slight disturbance in the physiological processes of an individual might cause premature regression of the corpora lutea. This would not be expected to interfere with gestation, since Herrick (1928) showed that live young could be produced by females from which both ovaries were removed after the twenty-seventh day of gestation.

Another very plausible explanation of the small corpora lutea counts may be obtained from the paper of MacLaren (1926), in which he reported finding in the uteri of pregnant guinea pigs placental remnants from pre-

ceding litters, which might have been confused with the deciduum type of dead foetuses. He states that these structures bore a close resemblance to actual embryos. Tho the litters used in this study were supposed to be first litters, some females no doubt became pregnant and aborted without any knowledge of it on the part of the experimenter.

Another plausible explanation involves the crossing over of ova from one horn of the uterus to the other, tho this has not been proven to occur in the guinea pig because of the capsule about the ovary and the difficulty of internal migration. In the sow, however, there is an internal migration to equalize the numbers in the two cornua. Corner (1921), Experiments of Kinney (1923) showed no migration in 23 guinea pigs having one ovary removed.

The six possible explanations for the occurrence of less foetuses than embryos may be given as follows:

I More than one ovum from a single follicle.

II Twinning.

III Failure of corpus luteum to develop after an ovum is discharged from the ovary.

IV Premature regression and absorption of the corpus luteum.

V Remnants of preceding pregnancy or the development of deciduomata which were confused with resorptions.

VI Migration of foetuses from one cornu to the other.

Table 14 has been prepared giving the number of corpora lutea found in each ovary, the number of foetuses in each cornu of the uterus together with the sex and designation of the number of resorptions, for each of the 13 females in which larger numbers of foetuses were observed than there were corpora lutea. The classification of the cause for the irregular count is given for each, together with pertinent remarks.

Table 14.

Exceptional Corpora Lutea Counts

Females: Identification No.	Females: Family	Mated with	Corpora lutea: Left ovary	Corpora lutea: Right ovary	Foetuses: Left cornu	Foetuses: Right cornu	Ova-Foetuses: Left side	Ova-Foetuses: Right side	Cause of irregular case	Remarks
169	2	♂35	0	3	1♀	3♀s	-1	0	III	
187	2	♂39	2	0	1♀	1♀	+1	-1	VI	
325	13	♂ 2	0	2	1R	1R 1♀	-1	0	IV	A small highly colored piece of lutein tissue in left ovary. Unquestioned resorption of the deciduum and button types.
240	13	♂32	0	0	1♀	0	-1	0	III	Remains of an old C.L.in rt.ovary
75	13	♂35	2	1	2♂s1♀ 1R	1R	-2	0	I	Could have been 2 sets of twins inn left cornu but no fusion of membranes R in left, deciduum; in rt, arm buds
125	13	♂35	0	1	1♂1R	1R	-2	0	III	R in left shows conspicuous membrane in rt a button
108	13	♂35	1	0	1♀	1R	0	-1	V	Large deciduum but no evidence of placenta
133	13	♂13	1	3	1♀ 1R	2♀s	-1	+1	VI	R of deciduum type
109	B	♂39	0	1	1R	1♂	-1	0	III	R is only deciduum and may be remnant V
105	CY-0	♂ 2	0	1	0	2♂s	0	-1	I	2 bodies in rt. ovary resembled matured follicles.
100	CY-0	♂ 2	0	1	1♀	1 ♀	-1	0	III	Left ovary small but normal
41	CY-1	♂13	3	0	2♂1♀	1R	0	-1	V	Unattached material resembling deciduum in rt cornu
123	CY-1	♂39	0	2	1R	2 ♀	-1	0	III	Decidua encased in old blood

♂ = male, ♂s = males
♀ = female, ♀s = females
R = Resorption
C.L. = Corpora lutea or corpus luteum
I, III, IV, V, VI refer to supposed explanation for apparent missing ova. See p. 202

The effort to classify the litters according to the cause of the irregular count is obviously subject to much question. For instance, failure of individual corpora lutea to develop would obviously explain all the cases, but litters were placed in this group only when there were no corpora lutea in the ovary in question. It was felt that if one corpus luteum was present in an ovary there was nothing physiologically wrong with the ovary so that corpora lutea could not develop and remain in it, and there was, therefore, some other cause for the lack of one or more corpora lutea.

The two litters assigned to crossing over of foetuses from one side to the other are extremely questionable because controlled experiments in which one ovary was removed have given negative results in the guinea pig, and the division between the two cornua of the uterus is extended so far posteriorly that foetuses would have to come practically out into the vagina to effect such a transfer internally. The membrane about the ovary is supposed to preclude external migration. These cases may be explained as due to the failure of individual corpora lutea to develop and the loss of one ovum from the other side.

Nothing was designated as a foetus which did not appear as such when the females were examined, but two of the resorptions were indicated as possible remnants. After examining the notes on these litters as a whole it is felt that some of the so called decidua were probably remnants of previous litters which were aborted or may have been resorbed. Of course failure of the corpora lutea to develop is also as satisfactory an explanation for these cases.

The two litters in which there were corpora lutea present, but not sufficient numbers for all of the foetuses, were considered as a result of more than one ovum coming from a single follicle. Twinning at a very early age, so that there was no connection between the membranes of the developing embryos, would explain these cases as well.

The one litter in which there was some lutein tissue found in the ovary was considered as being the results of premature regeneration of the corpus luteum.

Aside from the possible errors in the corpus luteum count as an indication of the number of ova produced which have been pointed out, there is also the probability of some corpora lutea resulting from follicles which practically mature and then become atresic without the ovum being shed. All of the conditions except the last would show a smaller mortality than actually occurred. There seems to be no basis for estimating the significance of these possible errors.

Finally it should be mentioned that the 13 exceptional litters showed a considerably higher mortality than was observed in the 338 other litters. In this group there were 24 corpora lutea found and there were 15 foetuses without corpora lutea on the same side. There were 11 dead foetuses and two missing ova. There was thus a 33 per cent mortality of the ova. This seems the most logical basis for calculating mortality in the exceptional cases. This suggests an association between foetal mortality and physiological disturbances in the ovary and the corpus luteum, and in the relation between the normal functioning of each.

Summary

Virgin females from different families were mated with males of each of 5 inbred families and killed just prior to parturition for a determination of the corpora lutea present in each ovary and the normal and abnormal embryos present in each cornu of the uterus. The following results were obtained:

1. Females of the different families, when mated with males from the various inbred families, showed considerable variation in the age at which first litters were conceived, but the average for the females of different families maintained practically the same relative order in all male pens.

2. While some differences in the potential capacity of the left and right ovaries to produce ova were indicated in certain families, the combined results indicated that there was some regulatory power limiting the total number of ova produced at a pregnancy, but the distribution of ova produced by each ovary was random.

3. The number of ova produced per pregnancy increased with the age of the dam at conception, the correlation being .34 ± .032 and the regression +.0865 young with each 20 days of age.

4. When corrections were made for age of conception the families ranked in about the same order for the numbers of corpora lutea produced per pregnancy as Wright (1922) found them to rank for size of litter, indicating that prenatal mortality is not sufficiently variable in the different families to change the order.

5. There were 8.70 ± .64 per cent of the ova from all females which were not represented by foetuses and there were 7.89 ± .61 per cent of the ova which were found as abnormal foetuses, making a total mortality of ova of 16.59 ± .85 per cent.

6. Females from all families showed high percentages of dead foetuses when mated with family 35 males, indicating the carrying of a lethal factor in the sperm of this family. Significant differences in the percentages of missing ova were observed between the families from which the females came, which is interpreted to indicate the production of non-viable ova. Family 13 and CY-2 females showed the largest percentages of missing ova.

7. Differences in the prenatal mortality in the left and right cornua of the uterus were not significant, but there was some indication that size of litter, the number of foetuses in a cornu, and the position which the foetus occupied had some effect.

8. The average number of ova produced per pregnancy and the prenatal mortality varied with the season, conceptions in April, May and June being most favorable. August, September and October were the least favorable for litter size, but the prenatal mortality was heaviest in January, February and March.

9. The character of the dead foetuses varied from remnants consisting only of the deciduum basilis to large almost full term foetuses which were edematous. Forty-eight of the sixty-nine dead foetuses found evidently died before the 20th day of gestation. Hemorrhage between the placenta and deciduum was a frequent cause of death in the larger embryos.

10. Indirect evidence did not indicate a greater mortality of one sex than of the other.

11. Thirteen females showed larger numbers of foetuses plus resorptions in one cornu than there were corpora lutea in the ovary on that side. Possible explanations of these are discussed.

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